MALACOLOGIA, 1970, 10(2) : 283–321

THE NEW ZEALAND SPECIES OF *POTAMOPYRGUS* (GASTROPODA: HYDROBIIDAE)

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ABSTRACT

In his revision of the genus, Suter (1905) recognized 6 species and 3 subspecies of *Potamopyrgus* from the 2 main islands of New Zealand, but the present study has shown that only 3 species exist. They are *P. antipodarum* (Gray, 1843), *P. pupoides* Hutton, 1882, and a previously unrecognized species **P. estuarinus** n. sp.

Potamopyrgus estuarinus and *P. pupoides* are oviparous, possess smooth, unornamented shells and are confined to brackish water, whereas *P. antipodarum* is ovoviviparous, highly variable in shell size, shape and ornamentation, and inhabits both fresh and brackish water. Populations of *P. antipodarum* may consist entirely of parthenogenetic females or contain varying numbers of sexually functional males. Rearing of *P. antipodarum* in the laboratory has shown that snails do not necessarily breed true with respect to shell ornamentation, and that shell shape and ornamentation are not controlled primarily by environmental factors. The shell of *P. estuarinus* is indistinguishable from shells of some *P. antipodarum*, but *P. pupoides* is easily recognized by its small, pupiform shell.

The radula, operculum, external morphology, body pigmentation and male reproductive system are similar in all species and do not provide useful taxonomic characters. In *Potamopyrgus antipodarum* the lower section of the female reproductive system is modified to form a brood pouch with the open sperm groove running along its floor. In *P. estuarinus* and *P. pupoides* the lower reproductive tract is dominated by the strongly developed capsule gland which is physically separated from the spermathecal duct below.

The diploid chromosome number of all 3 species is 24.

Ion-exchange chromatography of shell periostracal protein has disclosed no significant differences in amino acid composition between species, but considerable intraspecific variation is found.

Potamopyrgus antipodarum is abundant in permanent freshwaters of all kinds and has been found in water up to 26‰ salinity, although experimental work indicates that it is active only in water below 17·5‰ salinity. No clear relationship between shell morphology and type of habitat has been found. *P. estuarinus* is most abundant in tidal estuaries where considerable fluctuations in salinity are found, and where many snails are regularly exposed to the air for part of each tide cycle. *P. pupoides* occupies a similar habitat, but normally remains fully aquatic at all times. In the laboratory *P. estuarinus* and *P. pupoides* remained active at all salinities from fresh to sea water, but they have not been found in fresh water in the field.

Laboratory experiments have shown the existence of behavioural differences between species, which are associated with the different habitats occupied by them. *Potamopyrgus estuarinus* shows pronounced amphibious tendencies not found in *P. antipodarum* and was able to survive in a " dormant " state when exposed to the air for up to 70 days.

The *Potamopyrgus antipodarum* complex is examined in the light of current concepts of the species, and the high degree of variability found in this species is associated with

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the occurrences of ovoviviparity and parthenogenesis which allow a high degree of divergent evolution to occur independently in individual populations.

A comparison between *Potamopyrgus antipodarum* and the European species *P. jenkinsi* (Smith) shows that the 2 cannot be distinguished on anatomical grounds, and many features of their biology and ecology are similar. It therefore seems probable that the 2 are the same species, the European snails having been introduced from New Zealand (or Australia ?) in the 19th century.

INTRODUCTION

Two genera of Hydrobiidae, *Potamopyrgus* Stimpson 1865 and *Opacuincola* Ponder 1966 are recognised from New Zealand, the latter containing a single, recently discovered subterranean species (Ponder, 1966). The genus *Potamopyrgus* was erected for the New Zealand species *Melania corolla* Gould 1874, and was separated from other hydrobiid genera primarily on the basis of radular structure. This study has confirmed the generic distinctness of *Potamopyrgus*, but its relationships to other hydrobiid genera remain unclear. Taylor (1966) has suggested it may belong in his subfamily Littoridininae in which he places *Pyrgophorus* Ancey 1888, the other genus containing ovoviviparous, spiny-shelled snails, although differences in the verge of *Potamopyrgus* suggest that it is not close to the American hydrobiids familiar to him.

In 1882, Hutton assigned all the known New Zealand Hydrobiidae to *Potamopyrgus*, and in the most recent revision of the genus, Suter (1905) recognised 6 species and 3 subspecies, which he distinguished primarily on shell characters.

Suter's (1905) revision has remained the definitive systematic work on *Potamopyrgus* in New Zealand, but it is now clear that there is much greater variation in shell characteristics than was recognised by him. A thorough investigation of the systematics of *Potamopyrgus* in New Zealand has therefore been undertaken.

Snails were collected from 128 localities throughout the 2 main islands of New Zealand, and selected morphological, reproductive and biochemical factors, as well as environmental relationships have been examined.[2]

As a result of this study it is concluded that only 3 species can be recognised on the 2 main islands of New Zealand. In addition, 2 species, *Potamopyrgus dawbini* Powell 1955 and (?) *P. melvilli* (Hedley, 1916) have been described from the Auckland and Kermadec Islands respectively, and species probably referable to *Potamopyrgus* are found in southern and eastern Australia (Williams, 1968). A single species, *P. jenkinsi* (Smith) is widely distributed in Britain and Europe, and was probably introduced from Australasia in the late 19th century (Boettger, 1951; and this paper).

North American species formerly referred to *Potamopyrgus* are now placed in other genera (Morrison, 1939; Taylor, 1966) but the true generic status of central African snails placed in *Potamopyrgus* by Pilsbry & Bequaert (1927) remains problematical.

REVISED DIAGNOSIS OF *POTAMOPYRGUS*

Potamopyrgus Stimpson 1865

Type (Monotypy): *Melania corolla* Gould, 1847

Shell dextral; height less than 12 mm; shape variable ovateconical-cylindrical; up to eight whorls, ventricose-flat sided,

[2] The raw data on which this account is based may be found in the appendices to a thesis by the author deposited in the Massey University Library, Palmerston North, New Zealand.

smooth with or without shouldering and/or periostracal spines; body whorl over half height of shell; imperforate; aperture ovoid, continuous (in fully grown shells). Operculum ovate, thin, corneous, subspiral, usually possessing a calcareous smear. Radula taenioglossan; central tooth trapezoidal, inferior margin nearly straight, faintly trilobate, basal cups close to lateral margins; lateral tooth denticulate, shank 2–3 times length of subrhomboidal body which possesses no basal peg; marginals finely serrate, long and slender, shanks straight, sharply curved at free ends; cusp formula $\frac{(3-5)\ 1\ (3-5)}{(2-5)\quad\quad(2-5)}$: (7–13): (14–32): (21–48). Animal with long pointed tentacles. Reproduction sexual or parthenogenetic, ovoviviparous or oviparous. Males with long, narrow non-lobate penis containing a single duct, normally coiled beneath the mantle edge and attached to the head on right of middorsal line; vas deferens strongly coiled; prostate imbedded in visceral mass. Ovoviviparous females possess a thin walled brood pouch, with the sperm channel (=ventral channel) incorporated in its floor; oviparous females with the spermathecal duct separated from the accessory glands above, and probably functioning as the pallial oviduct. Habitat, fresh and brackish water.

Synonymy

Until further anatomical information is available the synonymy of other genera with *Potamopyrgus* must be considered tentative. Such genera may include *Austropyrgus* Cotton 1942 and *Fluviopupa* Pilsbry 1911.

DIAGNOSTIC CHARACTERS OF THE NEW ZEALAND SPECIES

Potamopyrgus antipodarum (Gray, 1843)

Amnicola antipodanum, Gray, 1843, *in* Dieffenbach, E., *Travels in New Zealand*, 2: 241 (New Zealand; British Museum).

Amnicola antipodarum, Gray, 1844, *Rev. Zool.*, 7: 356.

Hydrobia antipodum, von Martens, 1873, *Mal. Blätter*, 19: 14.

Hydrobia antipodum, Smith, 1875, *Zool. Voy. "Erebus" & "Terror"*, 2: 3.

Bythinella antipoda, Hutton, 1880, *Man. N.Z. Moll.*, p 81.

Potamopyrgus antipodum, Hutton, 1882, *Trans. N.Z. Inst.* 14: 145.

Potamopyrgus antipodarum, Hedley & Suter, 1893, *Proc. Linn. Soc. N.S.W.*, 7: 619.

Potamopyrgus antipodum, Suter, 1893, *J. Conchyliol.*, 41: 221.

Potamopyrgus antipodum, Suter, 1905, *Trans. N.Z. Inst.*, 37: 263.

Potamopyrgus antipodum zelandiae (Gray, 1843), Suter, 1905, *Trans. N.Z. Inst.*, 37: 263 (New Zealand; in British Museum).

Potamopyrgus corolla (Gould, 1847), Suter, 1905, *Trans. N.Z. Inst.*, 37: 260 (New Zealand; U.S. Nat. Museum).

Potamopyrgus badia (Gould, 1848), Suter, 1905, *Trans. N.Z. Inst.*, 37: 264 (Banks Peninsula, N.Z.; U.S. Nat. Museum).

Potamopyrgus egenus (Gould, 1848), Suter, 1905, *Trans. N.Z. Inst.*, 37: 265 (Banks Peninsula, N.Z.; U.S. Nat. Museum).

Potamopyrgus corolla salleana (Fischer, 1860), Suter, 1905, *Trans. N.Z. Inst.*, 37: 262 (New Zealand; collection of *J. de Conchyliologie*, Paris).

Potamopyrgus spelaeus (Frauenfeld, 1862), Suter, 1905 *Trans. N.Z. Inst.*, 37: 266 (caves, Collingwood, Nelson, N.Z.; K.K. Hofmuseum, Vienna).

Potamopyrgus subterraneus, Suter, 1905, *Trans. N.Z. Inst.*, 37: 267 (well, Ashburton, N.Z.; Dominion Museum, Wellington).

Holotype.—Deposited in the British Museum (Natural History).

Type Locality.—New Zealand, in fresh water.

A full account of all earlier synonymies and the nomenclatural histories of the species recognized by Suter (1905) is given in his paper and therefore is not repeated here. However, the full nomenclatural history of Suter's *Potamopyrgus antipodum* is given, as the valid spelling of the specific name has been in doubt. This is resolved as follows.

In his original description, Gray misspelled the specific name *antipodanum*. This was emended in a second description of the species the following year (Gray, 1844) and was also recognized as "an evident and accidental mis-spelling" by Hedley & Suter (1893). As Gray's original spelling was clearly an inadvertent error it should be corrected to *antipodarum*. The emendation of Gray's name to *antipodum* is not justified, and this spelling which has been followed by most subsequent authors should not be used.

Shell ovate-conic, height fully grown 3–12 mm; shape highly variable, slender and elongate to ventricose; spire long or short, loosely or tightly coiled, whorls 4–8 flattened to rounded, with or without shouldering and variable periostracal spination. Females ovoviviparous, the lower oviduct forming a brood pouch. Reproduction sexual or parthenogenetic, sex ratio variable. Inhabit fresh waters of practically every type and also brackish water, throughout New Zealand.

Potamopyrgus pupoides Hutton, 1882

Potamopyrgus pupoides, Hutton, 1882. *Trans. N.Z. Inst.*, 14: 146. (Heathcote estuary Christchurch; Canterbury Museum).
Potamopyrgus spelaeus pupoides (Hutton, 1882), Suter, 1905, *Trans. N.Z. Inst.*, 37: 266.

Holotype.—Deposited in the Canterbury Museum, Christchurch, New Zealand.
Type Locality.—Heathcote estuary, near Christchurch, New Zealand. In brackish water.

Shell height less than 2·5 mm, conic-cylindrical, obtuse in apical region; whorls 5, flat, smooth, never possessing spines or keels, suture often margined below. Reproduction sexual, females oviparous. Inhabits the brackish lower reaches of streams and rivers, and tidal estuaries, throughout New Zealand.

Potamopyrgus estuarinus n. sp.

Holotype: Deposited in Dominion Museum, Wellington, New Zealand.
Paratypes: Auckland, Dominion and Canterbury Museums, New Zealand; Naturhistoriska Museet, Goteborg, Sweden.
Type Locality: Small brackishwater stream, Bell Block, Taranaki, New Zealand.

Shell ovate-conic, height up to 7 mm; whorls 6–7, smooth, flattened; never possessing periostracal ornamentation; sutures sometimes margined below; apical whorls frequently eroded. Females oviparous, reproduction sexual. Rostral and mantle pigmentation always very dark. The ecological niche of this species is restricted and distinctive, snails inhabiting the lower tidal reaches of rivers, and particularly harbour mud flats adjacent to river mouths, where they are alternately exposed and covered by water of varying salinity.

The animals of dried specimens labelled *Amnicola antipodarum* in the U.S. National Museum were examined by Morrison (1939), who reported that the males possessed a long, simple, geniculate verge and the females were oviparous. This description indicates that they were my *Potamopyrgus estuarinus*. However, examination of a photograph of the holotype of *A. antipodarum* in the British Museum shows that it is definitely not *estuarinus* as it possesses a large, heavily built shell unlike that found in the latter and this is confirmed by Dr. R. K. Dell (pers. comm.) who has examined the type.

COMPARATIVE SYSTEMATIC ACCOUNT

Methods

Shell

Three shell parameters, height, width and height of aperture (Fig. 1a) were

measured to the nearest 0·1 mm, with a linear eyepiece micrometer inserted in a stereoscopic microscope at magnifications of ×12·5 and ×32. For comparative purposes, ratios of shell height to shell width (h/w) and shell height to aperture height (h/ap h) were employed, as well as direct comparisons of measurements. Shells of fully grown snails only were used in comparative studies. The number of snails measured from each population was determined partly by numbers available and in all cases was sufficient to give a thorough indication of the full range of variation found within the population. In most cases 10–20 snails were measured.

Whorl counts were made to the nearest complete whorl. Because the apex of many shells was eroded accurate whorl counts could not always be made.

Some shell characters such as convexity and shouldering of whorls, and degree of ornamentation cannot be expressed conveniently as measurements and so do not lend themselves to biometric examination. Comparisons of such characters were made from camera lucida tracings.

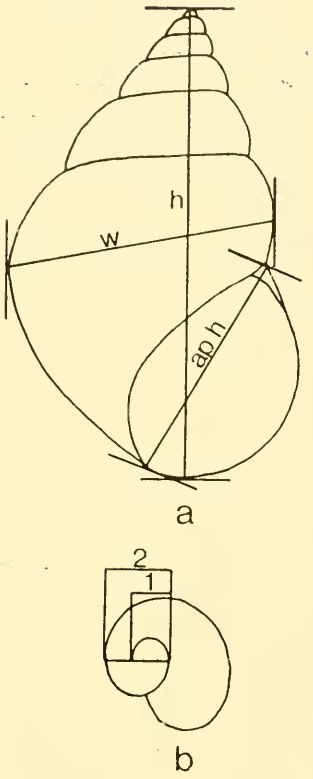


FIG. 1. Measurements made in the study of shell variation. **a.** Fully grown shell. **b.** Embryonic shell. h, shell height; w, shell width; ap h, aperture height; 1, width of tip of apical whorl; 2, diameter of first whorl.

Embryo shell

Embryos were taken from the brood pouches of individuals of *Potamopyrgus antipodarum* and camera lucida tracings of shell outlines were made at a magnification of ×120. From the shell tracings the width of the tip of the apical whorl, and the diameter of the first whorl were measured (Fig. 1b).

Operculum

Opercula were removed from snails and cleaned in a weak solution of oxalic acid. Permanent mounts were made in polyvinyl alcohol (PVA), and examined with a binocular microscope using both top and bottom lighting. Slides were placed on a dark background so that calcification within the operculum would be visible.

Radula

Radulae were extracted in boiling 4% KOH, stained in picric acid and permanently mounted in PVA. Some radulae were mounted intact, whereas the teeth of others were teased apart. Duplicate counts of cusps, denticles and serrations were made on at least 3 lateral, inner and outer marginal teeth from each radula. All measurements were made with a linear eyepiece micrometer at magnifications of ×100 and ×400.

Internal anatomy

Anatomy was examined by dissection and serial sections. The most successful dissections were carried out on fresh

material. Snails to be sectioned were fixed in Bouin's fluid, sections were cut at 5-10 μ, stained with Ehrlich's haematoxylin and counterstained with eosin.

Chromosome numbers

Chromosome numbers were determined using a squash technique.

Shells of freshly obtained snails were cracked and tissues were examined immediately without fixation, or were fixed for 24 hours at 4°C in Carnoy's fluid (ethyl alcohol: glacial acetic acid: chloroform, 6:1:3, v/v/v), and stored in 70% alcohol in a refrigerator until required.

Small pieces of testis and ovary (plus digestive gland) were separated and stained in acetic-orcein (1% orcein in 45% acetic acid) for 10–15 minutes on a cavity slide. Material was transferred to a plain microscope slide in a minimum of stain, gently squashed under a cover slip and examined microscopically using oil immersion at $\times 1000$ magnification.

Laboratory rearing of *Potamopyrgus antipodarum*

Potamopyrgus antipodarum was kept in the laboratory in transparent plastic boxes ($14 \times 11 \times 6$ cm) with loose fitting lids. Boxes were half filled with tap water, and each contained several grams of finely sieved pond mud and pieces of *Elodea canadensis*. No artificial aeration of the water was required. Water levels were maintained and small quantities of pond mud were added at infrequent intervals. Under these conditions growth of snails was continous and fairly rapid (minimum generation time 6 months), and embryos were released by large numbers of adult snails.

Amino acid composition of shell periostracal protein

The method of Ghiselin *et al.* (1967) was used for preparation and analysis of shell material. Snails were completely removed from their shells, or in some cases the animal was separated after decalcification, and the shells were thoroughly cleaned. Shells were decalcified in the presence of 10% trichloracetic acid solution by HCl, and the periostracum remaining was removed, washed and hydrolysed with 6N HCl at 110°C for 24 hours under vacuum. All samples consisted of periostracal material pooled from a number of snails. Amino acids were analysed using a Beckman/Spinco Model 120 amino acid analyser.

Salinity relations

Snails were kept in the laboratory at 11 salinities, 0, 10, 20—100% sea water, made up by diluting freshly collected sea water with distilled water. Salinities were checked by titration with silver nitrate. Ten fully-grown individuals of *Potamopyrgus estuarinus*, 10 of *P. pupoides* and 20 of *P. antipodarum*, half from freshwater and half from water of fluctuating salinity, were placed in glass bowls containing 200 ml of water, at each salinity. Snails were transferred direct to the experimental salinity from water taken from their natural habitats. All experiments were run at 18–20°C for 24 hours. At the end of an experiment all inactivated snails were transferred to water with a salinity of 3·5‰ and examined again after a further 24 hours. All experiments were run in duplicate.

Amphibious behaviour

Laboratory experiments were designed to compare the behaviour of *Potamopyrgus antipodarum* and *P. estuarinus* when offered a choice between submerged and exposed substrata. The experimental apparatus consisted of a rectangular plastic box ($20 \times 10 \times 7$ cm) with a cardboard floor covered in a layer of river mud forming a sloping "ramp". The floor was subdivided into 3 zones, a lower submerged section, an upper zone of

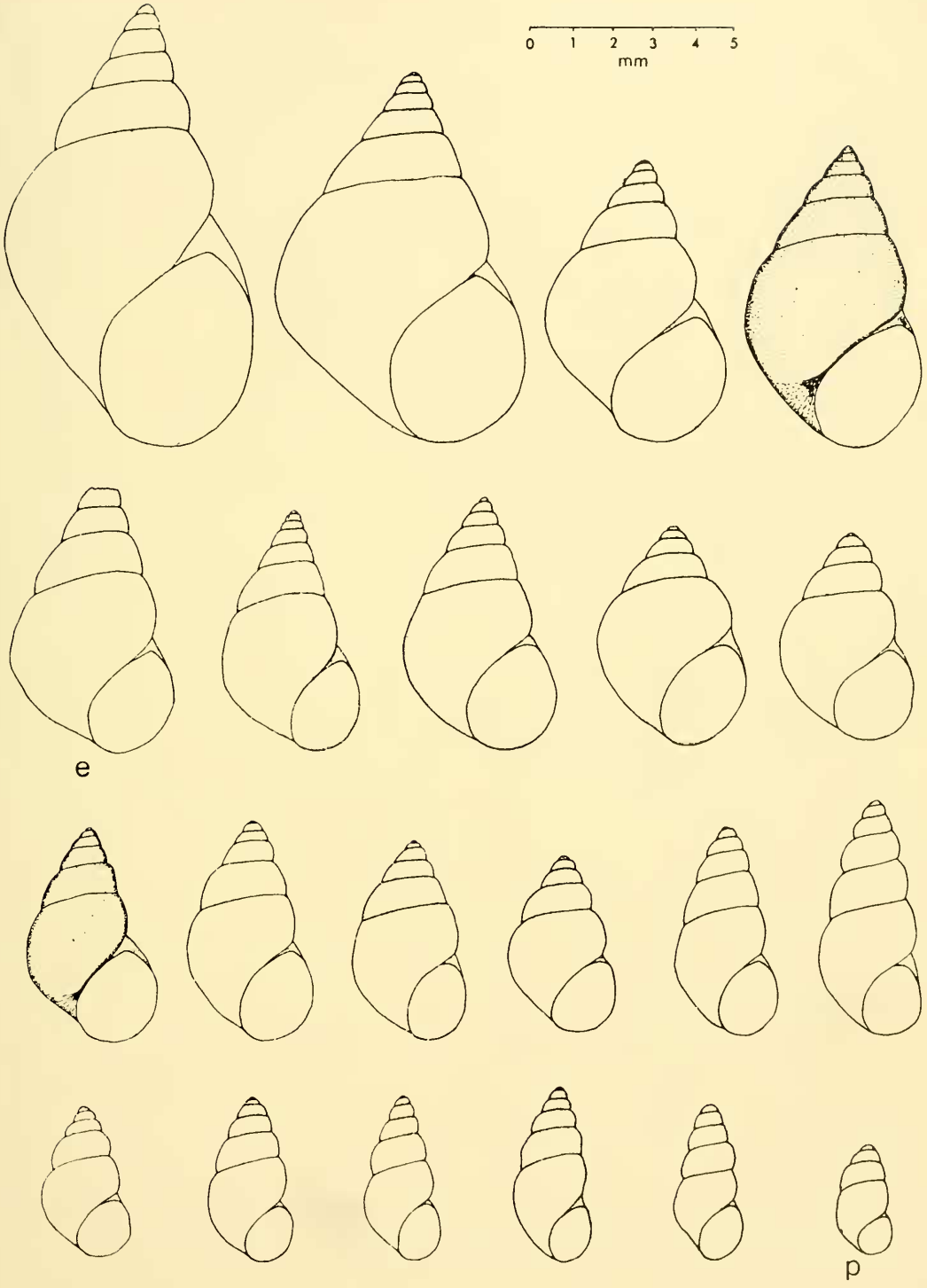


FIG. 2. Outline tracings of fully grown shells of *Potamopyrgus antipodarum* from 19 populations showing variations in size and shape. Typical shells of *P. estuarinus* (e), and *P. pupoides* (p) included for comparison.

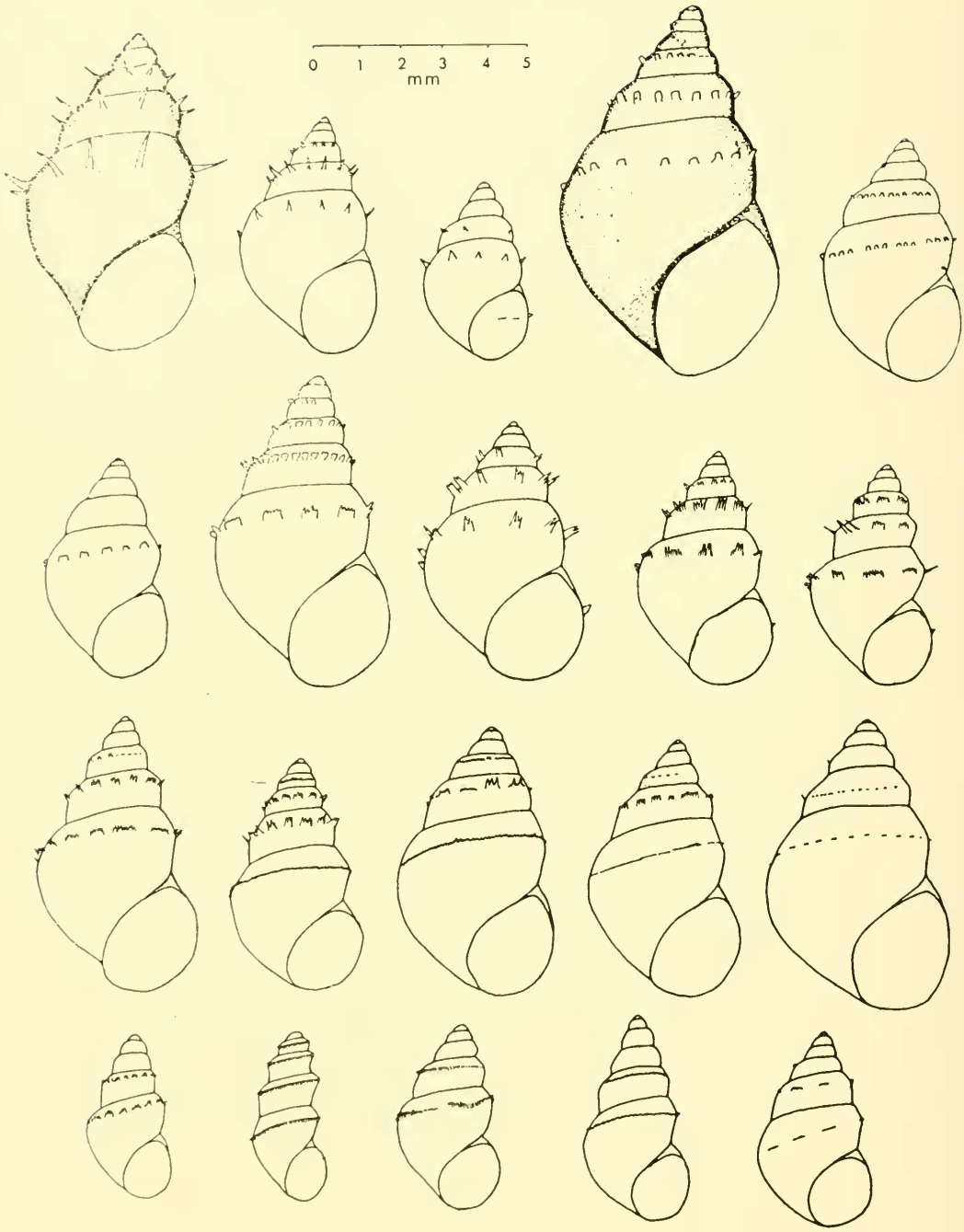


FIG. 3. Outline tracings of fully grown, ornamented shells of *Potamopyrgus antipodarum* from 20 populations, showing variations in size, shape and form of ornamentation.

slightly damp, exposed mud, and a middle zone of saturated mud also exposed to the air. One hundred snails were used in each experimental run. Tap water

was employed in experiments on both species and sea water was also used with *P. estuarinus*. The different salinities did not affect the responses of *P. estuarinus* in the experimental situation. All experiments were carried out at 18–20°C.

Effects of desiccation and starvation

(1) To determine the time snails can exist in a dry atmosphere before death occurs, experiments similar to those of van der Schalie & Getz (1963) were carried out. Shells of experimental snails were dried thoroughly with filter paper and placed in open, 9 cm diameter petri dishes which were kept in a desiccator containing calcium chloride as desiccant. The apparatus was maintained at 20–22°C

Fifty specimens of *Potamopyrgus estuarinus* and *P. antipodarum*, and 20 of *P. pupoides* were used in each experiment. Five individuals of each species were removed from the desiccator every hour for the first 3 hours, and then at 6 hour intervals until all were dead. A snail was considered dead if it showed no sign of movement within an hour of being placed in a shallow container of water.

(2) A permanently saturated atmosphere was produced in 9 cm covered petri dishes, by placing 6 thicknesses of water-soaked filter paper on the floor of each dish. As the petri dish lids were loose fitting, they permitted adequate gaseous exchange with the outside atmosphere. Dishes were kept at 20–25°C. In each experiment 40 individuals of each species were employed. Snails were examined daily to determine whether they were dead or alive, until all had died, or for 56 days in the case of *Potamopyrgus estuarinus*, and then after 70 days. Death was not easy to determine towards the end of the experiment, as with an increase in time the snails gradually withdrew further into their shells, until in many cases the operculum could no longer be seen. A snail was considered dead when no withdrawal reaction was elicited upon prodding the operculum firmly with a needle, or when signs of putrefying tissue were visible around the aperture of strongly withdrawn individuals.

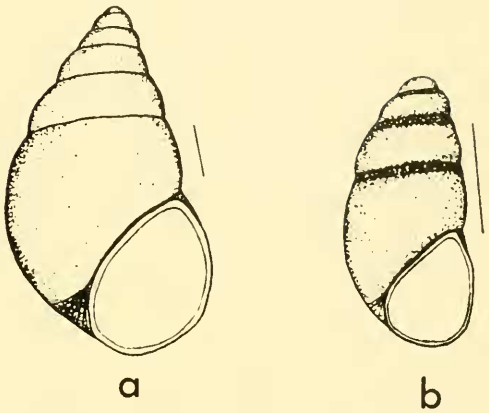


FIG. 4. Outline tracings of typical shells of **a**, *Potamopyrgus estuarinus* (from the type locality) and **b**, *P. pupoides*.

Results

Shell

Shells of the New Zealand species of *Potamopyrgus* are small and plain (apart from periostracal ornamentation), and offer few useful taxonomic characters. Shells of *P. antipodarum* are illustrated in Figs. 2 and 3, and of *P. estuarinus* and *P. pupoides* in Fig. 4.

Size and shape

Shell size, shape and variability within and between populations were examined biometrically by measuring shell height, shell width, aperture height and whorl number. It was reasoned that by comparing these parameters from a large number of populations, the nature of the shell variation, i.e., whether continuous or discontinuous variation existed, within

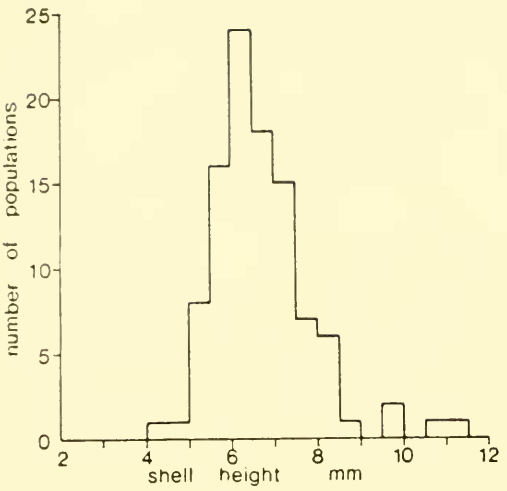


FIG. 5. Maximum height of shells in 100 populations of *Potamopyrgus antipodarum*.

the *Potamopyrgus* complex could be determined. Any discontinuities thus found might be indicative of separate lower taxonomic units which could be investigated further.

Maximum shell height in populations of *Potamopyrgus antipodarum* ranged from 4–11·5 mm. When the frequency of these heights is plotted (Fig. 5), the distribution is approximately normal and possesses a single peak at 6–6·6 mm, 72% of the values lying between 5·5–7·5 mm. By contrast, shells of the other 2 species are more uniform in height, those of *P. estuarinus* ranging from 5·5–7·5 mm and those of *P. pupoides*, 2·5–3 mm.

Shell ratios (h:aph, h:w) from selected populations of the 3 species are compared in Figs. 6 and 7. The populations are arranged in order of increasing mean h:aph ratios, and little correlation between aperture height and shell width is apparent. Mean shell ratios for all populations of *Potamopyrgus antipodarum* are plotted in Fig. 8, and the range of variation of these ratios within populations is shown in Fig. 9. Although the shells of some populations of *P. antipodarum* are so unlike that they could be considered sub-specifically different (Mayr *et al.*, 1953), it is clear that continuous variation in shell shape is found within this species. By comparison, only limited variability is exhibited by the shells of *P. estuarinus* and *P. pupoides*.

Numbers of whorls in fully-grown shells from 100 populations of *Potamopyrgus antipodarum* are shown in Table 1. Again there is considerable variation between populations but no clear division into discrete groups is found. As a general rule, the taller the shell, the more whorls developed.

To summarize, measurement of shell parameters has not provided evidence of clearcut morphological groups existing within the *Potamopyrgus antipodarum* complex, but rather has shown the existence of continuous variation of size and shape within this species. *P. pupoides* is distinguished by its small, pupiform shell, but the shell of *P. estuarinus* is indistinguishable from those of some forms of *P. antipodarum*.

Ornamentation

The presence or absence of spines or keels has been considered important in the separation and identification of the New Zealand species of *Potamopyrgus* (Suter, 1905). However, field observations made during the course of this study have shown that within the *P. antipodarum* complex considerable variation in degree and nature of shell ornamentation is found, even, in many cases, within a single population (Fig. 10). Ornamentation is purely periostracal, and no calcium is found in the spines.

Potamopyrgus antipodarum was reared in the laboratory in order that shell form and ornamentation of progeny of known parent snails could be examined. Some investigators (Dell, 1953; Hunter, 1961) have considered that much shell variation

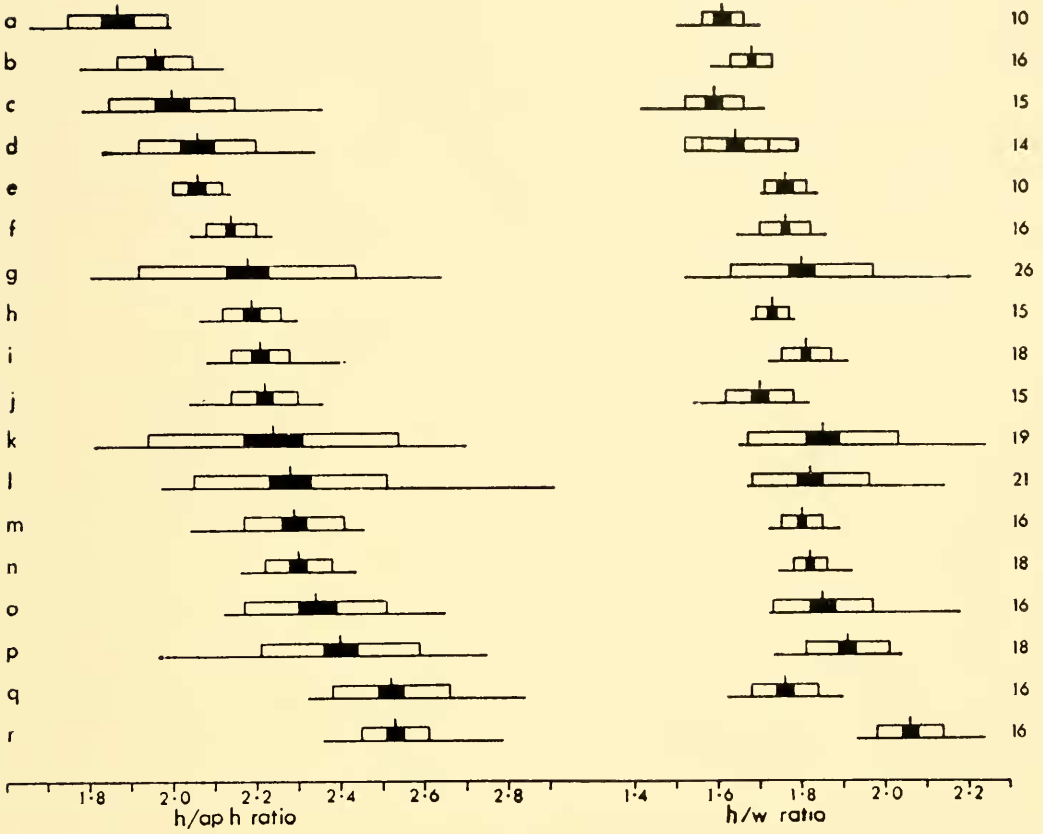


FIG. 6. Variation in shell height: shell width (h:w) ratio, and shell height: aperture height (h:aph) ratio in 18 populations of *Potamopyrgus antipodarum*. horizontal bar=range; open rectangle=1 SD; closed rectangle=1 SE; vertical bar=mean; numbers at right are sample sizes.

is the result of exposure to different environmental conditions, and this was observed in *Lymnaea tomentosa* reared in the laboratory under different conditions (Boray & McMichael, 1961).

In this study the experimental situation was reversed, and snails taken from differing environments were reared in the laboratory under identical conditions. Experimental populations were maintained for up to 3 years.

In the first series of rearings 711 progeny of 32 parthenogenetic snails from 12 populations were examined. Of 14 smooth-shelled parent snails, 9 produced totally smooth young, and 5 both smooth and spiny young. No smooth parent produced only spiny progeny. Of 18 spiny adult snails, however, only 3 produced all spiny young, 3 produced both smooth and spiny young, and 12 produced smooth young. In all cases, snails from natural populations consisting solely of smooth-shelled snails bred true in the laboratory, but this did not always hold for spiny-shelled snails.

As snails from different populations were reared under identical laboratory

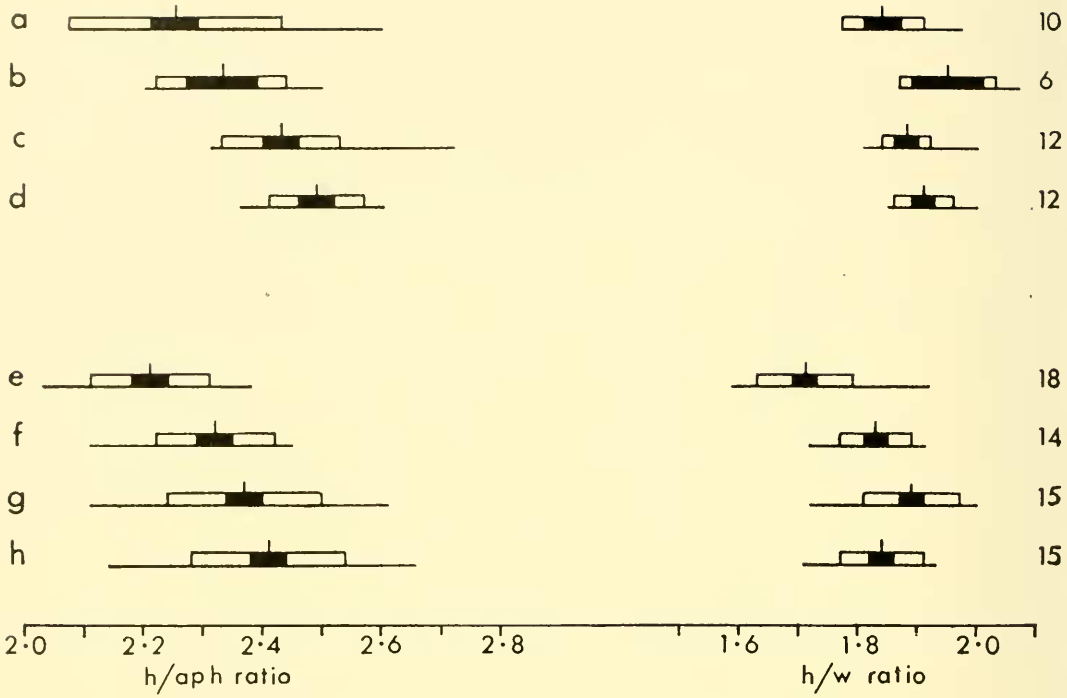


FIG. 7. Variation in shell height: shell width ratio, and shell height: aperture height ratio in populations of *Potamopyrgus pupoides* (a–d) and *P. estuarinus* (e–h).

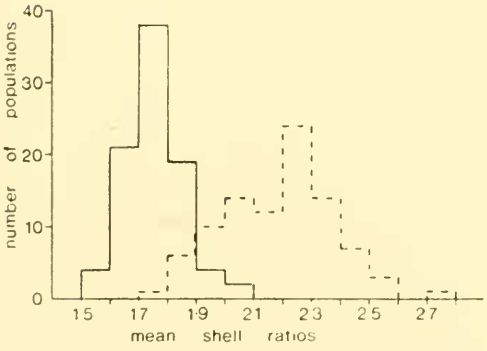


FIG. 8. Mean shell height : shell width ratios, and mean shell height : aperture height ratios in populations of *Potamopyrgus antipodarum*. Broken line=h: aph ratio; solid line=h: w ratio.

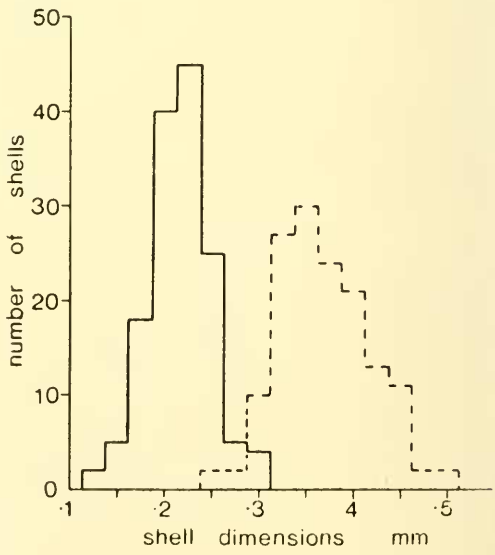


FIG. 9. Range of variation in shell height: shell width ratio, and shell height: aperture height ratio in 95 populations of *Potamopyrgus antipodarum*. Broken line=h:aph ratio; solid line=h:w ratio. A minimum of 10 shells were measured in all populations.

Erratum

The figure shown for Fig. 9 (p 294) is incorrect. The correct figure is shown below.

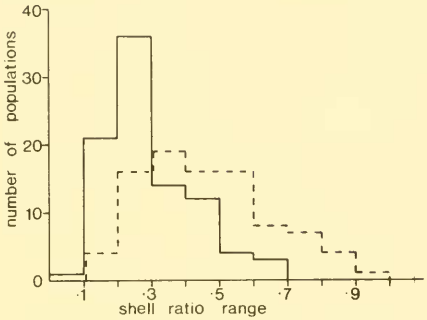


FIG. 9. Range of variation in shell height : shell width ratio, and shell height : aperture height ratio in 95 populations of *Potamopyrgus antipodarum*. Broken line = h:aph ratio; solid line = h:w ratio. A minimum of 10 shells were measured in all populations.

The figure shown for Fig. 19 (p 315) is incorrect. The correct figure is shown below.

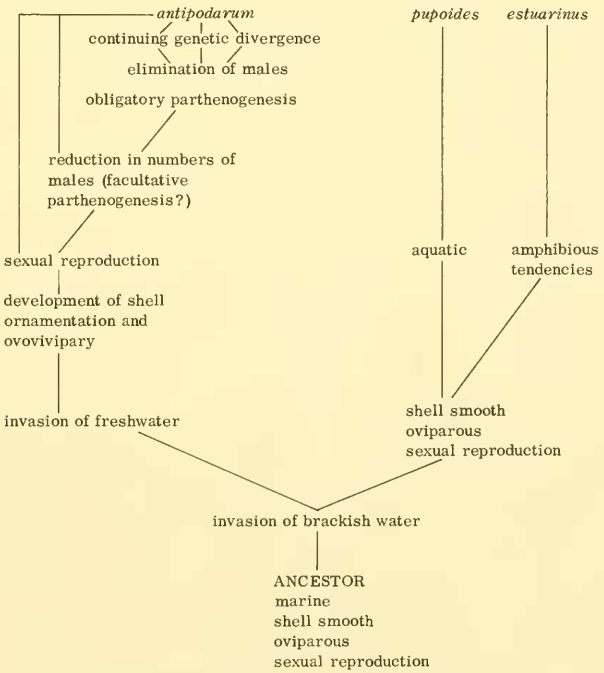


FIG. 19. Postulated steps in the evolution of the New Zealand species of *Potamopyrgus*.

TABLE 1. Numbers of whorls in fully-grown shells from 100 populations of *Potamopyrgus antipodarum*.

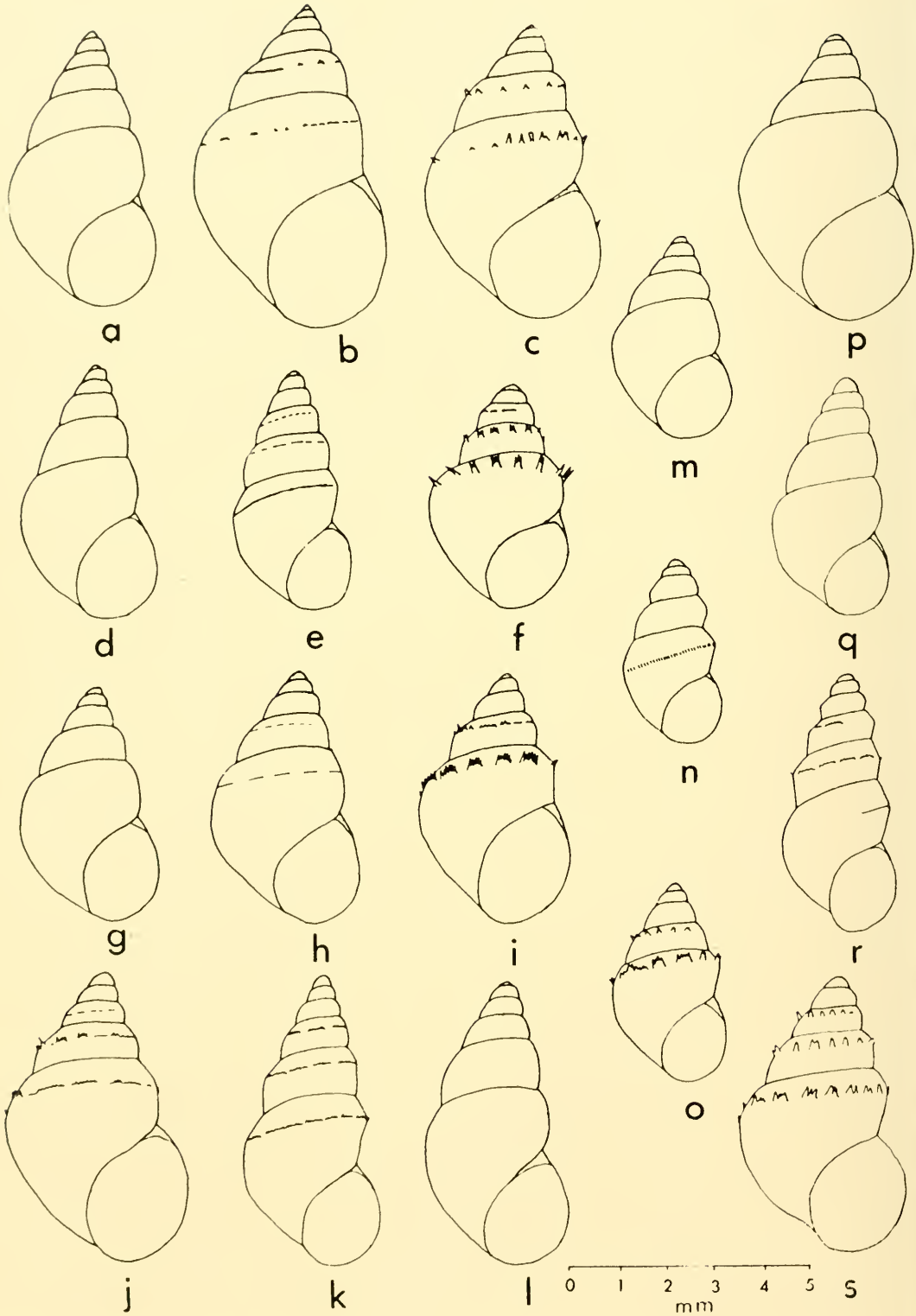
Shell height in mm	No. of Whorls					Totals
	4	5	6	7	8	
3–3·9	1	13	1	...	...	14
4–4·9	...	23	30	1	...	54
5–5·9	1	4	15	2	...	22
6–6·9	...	1	5	1	...	7
7–7·9	...	...	1	...	...	1
8–8·9	...	...	...	...	1	1
Totals	2	41	52	4	1	100

TABLE 2. Results of rearings from parthenogenetic individuals of *Potamopyrgus antipodarum* obtained from a pond at Massey University.

P_1*	F_1*		P_2*	F_2		P_3	F_3	
	Smooth	Spiny		Smooth	Spiny		Smooth	Spiny
Smooth	4	1	Smooth	35	0	...	...	
			Smooth	0	37	Spiny	2	3
						Spiny	0	10
						Spiny	0	22
			Smooth	43	0			
			Spiny	4	20	Spiny	0	33
						Spiny	0	10
						Spiny	0	16
Spiny	21	20	Smooth	43	0			
			Smooth	12	0			
			Smooth	5	0			
			Smooth	6	0			
			Smooth	20	0			
Spiny	56	3						
Smooth†	92	0	Smooth	25	0	Smooth	11	0
			Smooth	24	0			
			Smooth	35	0			
			Smooth	27	0			
			Smooth	20	0			
			Smooth	8	0			

*P=parent; F=offspring.

†4 snails kept together.


a
b
c
p
m
d
e
f
q
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g
h
i
r
o
j
k
l
s
0 1 2 3 4 5
mm

conditions, it is impossible to infer environmental influences as the only factors determining shell ornamentation. This must therefore have a genetic basis.

A longer term experiment was carried out using parthenogenetic snails taken from a pond at Massey University, Palmerston North, in which smooth and spiny shelled snails were present in approximately equal numbers. All generations were kept under identical experimental conditions but again a considerable amount of variation in shell ornamentations was found between the progeny of siblings, and between generations (Table 2).

A possible genetic basis for shell polymorphism in *Potamopyrgus jenkinsi* and *P. antipodarum* is suggested as follows. Ornamentation may be under polygenic control rather than determined by a single pair of alleles, and the expression of different degrees of shell ornamentation could result from interaction between environmental factors and the genomes of shell secreting cells in the mantle. Characteristically, only a part of a cell's genome is manifest at any one time, and environmental changes could modify and direct gene function producing phenotypic differences, e.g., inducing spine development, when the correct genes were active. Such a mechanism could account for the intra-specific variation in shell ornamentation which is frequently found and which cannot be explained in simple Mendelian terms or as solely environmentally controlled changes of the phenotype.

In contrast to shell ornamentation, the shell shape, height, whorl convexity and ratios of shell parameters of progeny in all laboratory populations closely resembled those of the parent. Range of shell variation between daughter snails was slight, and less than that found in samples of randomly selected adult snails from the original habitats.

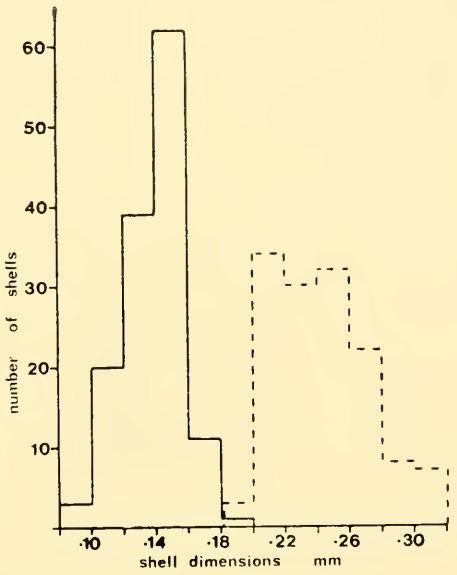

FIG. 11. Whorl measurements of 136 embryonic shells from 19 populations of *Potamopyrgus antipodarum*. Broken line=diameter of first whorl; solid line=width of tip of apical whorl.

Embryonic shell

The shells of embryos contained in the brood pouch of *Potamopyrgus antipodarum* are semi-transparent and possess no ornamentation, although transverse growth rings are visible (Fig. 12 c-e). The embryonic shell possesses 1·5 whorls when released from the brood pouch, and in older snails these whorls cannot be differentiated from later developed shell.

The width of the tip of the apical whorl and the diameter of the first whorl of 136 embryonic shells from 19 populations of *Potamopyrgus antipodarum* are plotted in Fig. 11. No indication of the presence of distinct size groups is found.

FIG. 10. Variation in shell shape and ornamentation in 6 populations of *Potamopyrgus antipodarum* 1, a–c; 2, d f; 3, g–i; 4, j–l; 5, m–o; 6, p–s.

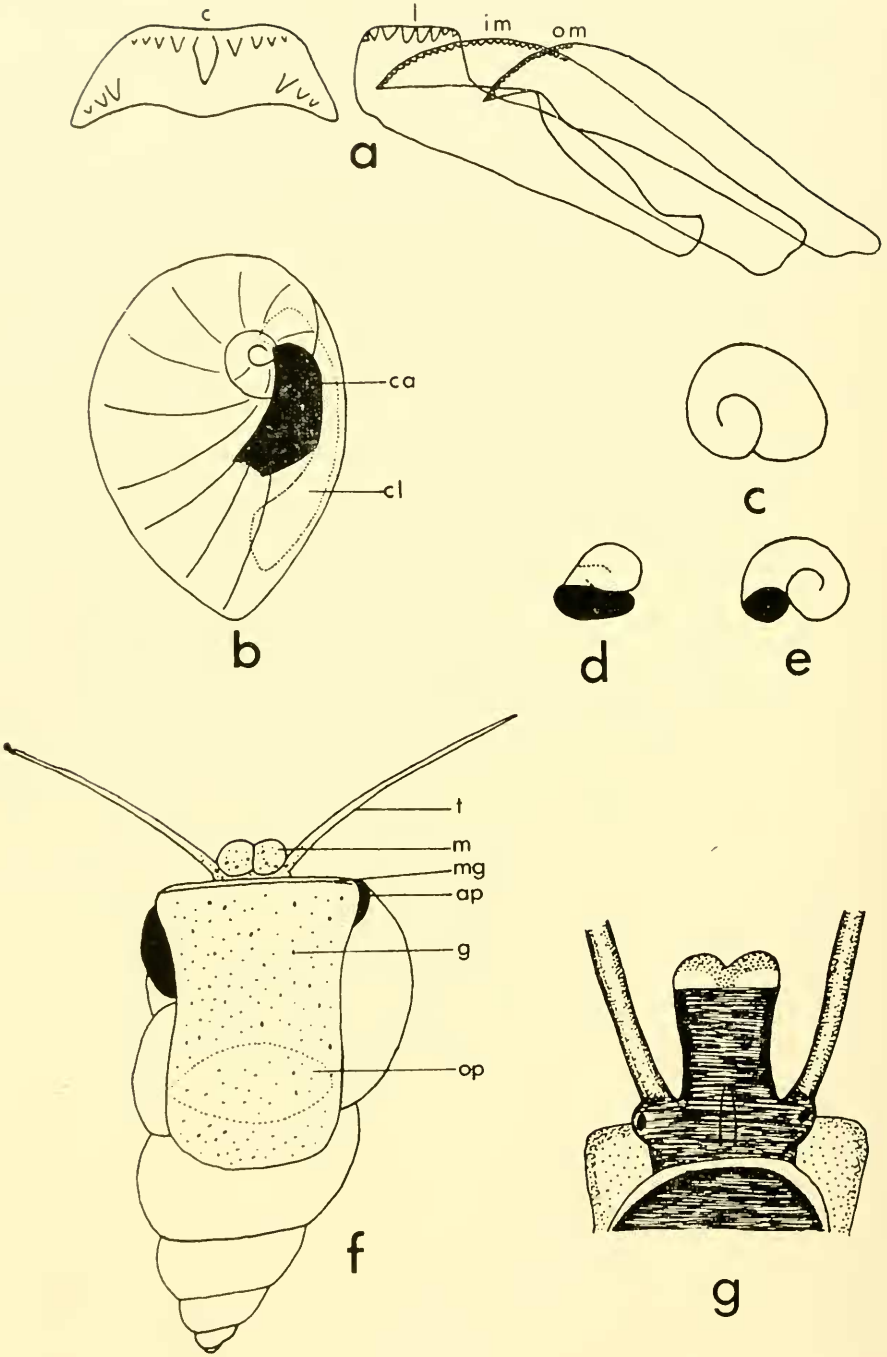

FIG. 12. Externals and radula of *Potamopyrgus antipodarum*. a, Radular teeth. b, Operculum (outer side). c–e, Embryonic shells from brood pouch. f, Animal extended (ventral). g, Head pigmentation. c = central; l = lateral; im = inner marginal; om = outer marginal; ca = calcareous smear; cl = clear area; t = tentacle; m = mouth lobe; mg = mucous groove; ap = aperture; g = granule; op = position of operculum.

TABLE 3. Variation in whorl dimensions of embryonic shells from 4 populations of *Potamopyrgus antipodarum*.

Locality	No. of shells measured	Width of apical tip (mm)	Diameter of 1st whorl (mm)
Lake Rotoiti	10	0·10—0·13	0·21—0·23
Lake Pupuke	10	0·11—0·16	0·21—0·23
Mt. Wharite	10	0·09—0·16	0·20—0·27
Lindis Pass	10	0·13—0·16	0·25—0·31

The range of variation in whorl measurements found in embryonic shells from 4 populations is given in Table 3. Clearly intrapopulation size variations can be almost as great as variations between populations.

Operculum

Stimpson (1865) described the operculum of *Potamopyrgus* simply as corneous, and Suter (1913) did not elaborate further. The following more detailed description is based on an examination of opercula from 30 populations of *P. antipodarum*, 3 of *P. estuarinus* and 3 of *P. pupoides*.

The ovoid operculum (Fig. 12b) is semi-transparent, its colour ranging from yellow to brown. The nucleus is subcentral, subspiral growth lines are clearly visible and there is no distinct marginal area. The muscle insertion area is indistinct but a narrow, clear, quasicrescentic area extending over half the length of the operculum is present close to the inner margin. The clarity of this area is somewhat variable. A small, irregularly shaped, calcareous smear is usually present to the right of the nucleus. The extent and degree of calcification is also variable but is clearly visible when the operculum is viewed with top lighting against a dark background. The operculum is of no value in distinguishing the New Zealand species of *Potamopyrgus*.

Radula

The radula of *Potamopyrgus* is taenioglossan. No important differences in general tooth shape are found between species, and representative teeth are illustrated in Fig. 12a. Within populations, slight variations may be found in the positions of the teeth on the radular ribbon with respect to one another. Some individuals have a clear space between the central and lateral teeth, but in others, no gap is found. Radular length generally increases with snail size (Fig. 13).

In all 3 species radulae of fully grown individuals examined possessed 62–93 rows of teeth. The rows are closer together in *Potamopyrgus pupoides* than in *P. antipodarum* or *P. estuarinus* (Fig. 14).

Cusp formulae for the 3 species are given below. These are based on an examination of snails from 28 populations of *Potamopyrgus antipodarum*, 3 of *P. pupoides* and 3 of *P. estuarinus*.

P. pupoides

$$\frac{(4\text{–}5)\text{—}1\text{—}(4\text{–}5)}{(4\text{–}5)\ \text{—}\ (4\text{–}5)} : 9\text{–}11 : 21\text{–}25 : 29\text{–}30$$

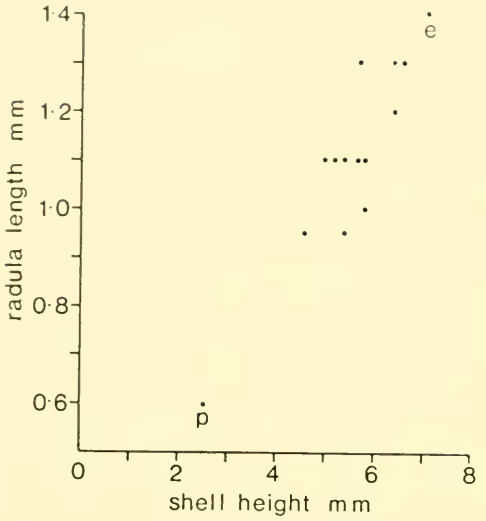

FIG. 13. Radular length plotted against shell height in 14 populations of *Potamopyrgus*. p = *P. pupoides*; e = *P. estuarinus*; other points = *P. antipodarum*.

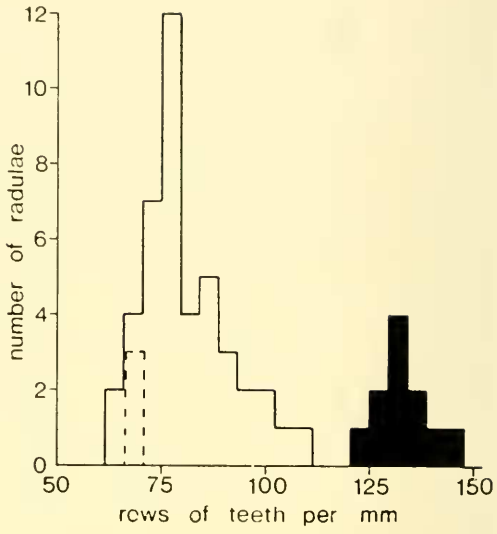

FIG. 14. Numbers of rows of teeth per mm of radular ribbon in the 3 species of *Potamopyrgus*. Broken line = *P. estuarinus*; solid line = *P. antipodarum*; solid histogram = *P. pupoides*.

P. estuarinus

$$\frac{(3\text{–}4)\text{—}1\text{—}(3\text{–}4)}{3\ \text{—}\ 3} : 8\text{–}9 : 14\text{–}19 : 21\text{–}35$$

P. antipodarum

$$\frac{(3\text{–}5)\text{—}1\text{—}(3\text{–}5)}{(3\text{–}5)\ \text{—}\ (3\text{–}5)} : 7\text{–}13 : 15\text{–}32 : 24\text{–}48$$

Results of a study of cusp variation in 3 populations of *Potamopyrgus antipodarum* are presented in Table 4. Cusp formulae vary considerably and in *P. antipodarum* this variation appears to be independent of variations in shell characteristics. *P. pupoides* can be distinguished using radular characters, (smaller, and the rows of teeth are closer together), but *P. estuarinus* and *P. antipodarum* possess sufficient variability in shape, cusp formulae and radula length: shell length ratios to prevent specific differences from being defined.

Hutton's (1882) cusp formulae for 4 New Zealand "species" cannot be given the diagnostic importance he gave them. The minor variations in tooth shape shown in his figures appear to have been produced by orientation of the radulae for illustration rather than by true structural differences and the dimensions he provided are far too large. Ponder's (1967) figure of the radula of "*Potamopyrgus antipodum*" (actually *P. estuarinus*; Ponder, pers. comm.) is also inaccurate.

Externals of animal

The external appearance of the 3 species is identical (Fig. 12 f, g) except for differences in size and intensity of head and mantle pigmentation. The following description therefore applies to all 3 species.

The tentacles are long and slender, clear, with black pigment distributed as in Fig. 12g. The eyes have prominent pigment cups and are located in bulges at the bases of the tentacles. They are not borne on prominent tubercles as described by Morrison (1939). Rostral pigment is distributed in fine transverse

TABLE 4. Variation in numbers of cusps, denticles and serrations on the radular teeth of *Potamopyrgus antipodarum* from 3 populations.*

Locality	Central	Lateral	Inner Marginal	Outer Marginal
Massey University	(4–5)–1–(4–5) / (3–4)–(3–4)	9–11	20–25	31–47
Tiritea Stream	5–1–5 / (3–4)–(3–4)	9–11	25–35	32–45
Makara	(4–5)–1–(4–5) / (3–4)–(3–4)	9–11	21–29	32–42

* Examination of 12 snails per population making duplicate counts of cusps, denticles and serrations on at least 3 teeth per row per radula.

bands, is dark and evenly dispersed in *Potamopyrgus pupoides* and *P. estuarinus*, but is often lighter and more variable in *P. antipodarum*. The mouth lobes are white and normally have grey, crescentic markings dorsally. Pigmentation of the head behind the level of the eyes is always dark and the buccal mass is often visible dorsally near the base of the rostrum. The broad, grey foot has a stippled appearance, is rounded posteriorly and truncated anteriorly. The anterior margin is nearly straight, and the antero-lateral angles are somewhat auriculated. The anterior mucus slit is prominent and extends the width of the foot. The mantle skirt is black, with a well defined, pale, anterior margin. Large numbers of shiny white " granules " are found in the foot and mantle edge, and frequently in the mouth lobes and tentacles close to the eyes.

Although both Fretter & Graham (1962) and Muus (1963) consider that head pigmentation is distinctive in different species of European Hydrobiidae, and a useful aid in identification, no consistent differences in pigment distribution have been found between the New Zealand species of *Potamopyrgus*. Also, no correlation has been found between pigment intensity and shell form in *P. antipodarum* as has been suggested may occur in *P. jenkinsi* (Warwick, 1952).

Reproduction

Sex ratio

Morrison (1939) found that the specimens of " *Annicola antipodarum* " he examined possessed sexual reproduction and were oviparous, and he assumed that all the New Zealand species of *Potamopyrgus* reproduced in this way. Later writers, however, apparently unaware of Morrison's study, have assumed them all to be viviparous (Marples, 1962; Dell, 1969), and apart from *P. pupoides*, parthenogenetic (Ponder, 1966).

The present investigation has shown that none of the New Zealand species consists solely of parthenogenetic females, and that males are relatively common in all 3 species.

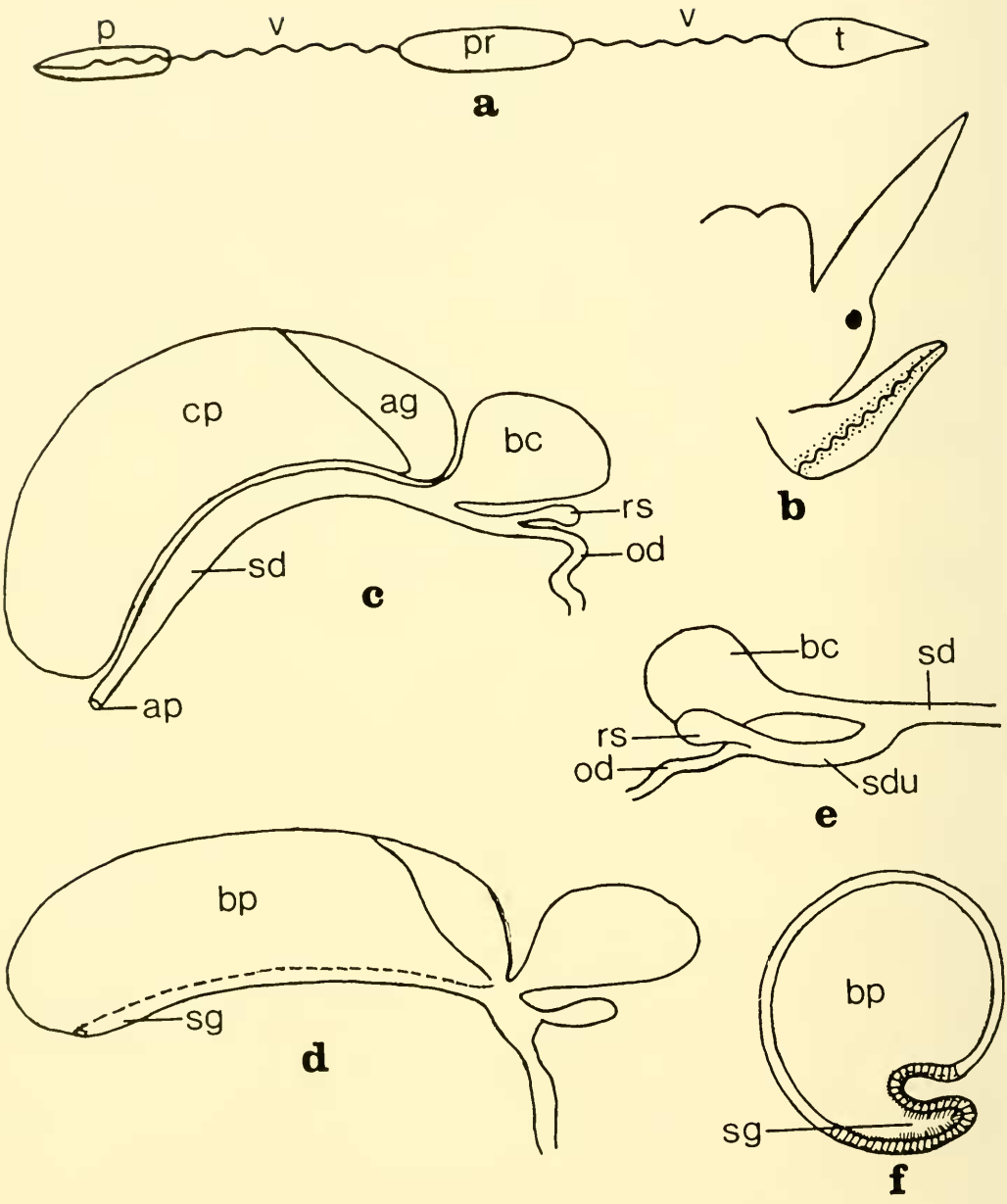

FIG. 15. Reproductive system. **a**, diagramatic representation of male system. **b**, penis. **c**, diagramatic representation of female system of *Potamopyrgus estuarinus* and *P. pupoides*. **d**, diagramatic representation of female system of *P. antipodarum*. **e**, arrangement of ducts in region of the bursa in *P. estuarinus*. **f**, Transverse section of empty brood pouch of *P. antipodarum* showing position of sperm groove. p=penis; pr=prostate; t=testis; v=vas deferens; ag=albumen gland; ap=female opening to pallial cavity; bc=bursa copulatrix; bp=brood pouch; cp=capsule gland; od=oviduct; rs=receptaculum seminis; sd=spermathecal duct; sdu=sperm duct; sg=sperm groove.

TABLE 5. Dimensions of sperms of New Zealand species of *Potamopyrgus* compared with those of 2 species of European Hydrobiidae.

Species	Total length (microns)	Head length (microns)	Reference
P. antipodarum	110	3	Present study
P. estuarinus	140	3	Present study
P. pupoides	110–120	3	Present study
P. jenkinsi	40	4–6	Patil (1958)
Hydrobia ulvae	100	?	Patil (1958)

An initial investigation into the occurrence of males was made by examining 6–10 individuals from each of 63 populations of *Potamopyrgus antipodarum*, 5 of *P. estuarinus* and 3 of *P. pupoides*. Males were found in all populations of the 2 latter species and in 24% of *P. antipodarum* populations.

In a more comprehensive study, 50–200 snails were examined from selected populations. Males were found in 9 out of 24 populations of *Potamopyrgus antipodarum*, and in 7 of these they constituted less than half of the total sample. (In populations in which males occurred they represented 2–52%, mean=29%, of snails examined.) In *P. estuarinus* 36–58% of population samples were males, and in *P. pupoides* males constituted 10–28% of population numbers.

Male reproductive system

The gross anatomy of the male reproductive system is identical in all 3 species (Fig. 15a) and closely resembles that of *Potamopyrgus jenkinsi* as described by Patil (1958). The testis lies in the upper whorls of the shell on the columella side, and from it arises the vas deferens, a narrow, highly convoluted tube with a thin, muscular wall. It passes through a large prostate gland embedded in the tissues of the visceral mass at the posterior end of the body whorl, and finally runs forward on the head, close to the skin, to the penis, opening at its tip. No proximal dilation of the vas deferens, as described in *P. jenkinsi* by Patil, was found. In all 3 species the vas deferens of mature individuals is normally packed with living sperm throughout its entire length and consequently has a conspicuous white appearance.

Sperms have slender, conical heads and long, lash-like tails, and are all of the one kind. Their dimensions (living) are given in Table 5 in which comparisons are made with the sperm of *Potamopyrgus jenkinsi* and *Hydrobia ulvae*.

The sperms of the New Zealand species are comparable in length to those of *Hydrobia ulvae* but are 2–4 times as long as those described for *P. jenkinsi*. As the sperm of *P. jenkinsi* was observed in sectioned material, however, it is possible that the dimensions given are not a good indication of their length in life.

The penis (Fig. 15b) is situated on the right side of the head beneath the mantle edge. It is simple in form, tapering at its tip and bears no accessory lobes. In life

it is colourless and semi-translucent, the vas deferens being visible within. It is capable of considerable contraction and expansion, and when contracted the walls near its base have a telescopic appearance. In preserved specimens the shape and orientation of the penis tend to vary considerably, and usually it becomes somewhat coiled, especially towards the tip.

The penis is of no value as a taxonomic character for differentiating between New Zealand species of *Potamopyrgus*.

Female reproductive system

The structure of the female reproductive system divides the New Zealand species of *Potamopyrgus* into 2 distinct groups which possess major differences in the form of the lower section of the oviduct, and its associated glands.

(1) *Potamopyrgus antipodarum* (Fig. 15d)

The ovary is situated on the columellar side of the digestive gland in the apical whorls, and reaches almost to the tip of the spire. It has a white, rather lumpy appearance when mature, and contrasts strongly in colour with the brownish digestive gland which has a stippled appearance. The oviduct leading from it is slender and thin walled, but its walls become greatly thickened in the region of the bursa copulatrix and receptaculum seminis. Anteriorly, the reproductive system consists of the pallial oviduct which has a prominent, clearly demarcated groove, the sperm channel, on its ventral surface (Fig. 15f). In immature individuals the thin walled lower oviduct is circular in cross section but in mature snails it becomes greatly enlarged and distended to form a brood pouch within which over 100 embryos in various stages of development may be found. The sperm channel leads directly to the very large bursa copulatrix and via the sperm duct to the smaller receptaculum seminis. Both normally function to store sperm (Fretter & Graham, 1962), but must have lost this function in parthenogenetic individuals. Fretter and Graham have suggested that the well developed bursa copulatrix of *Potamopyrgus jenkinsi* may act as a waste dump for excess egg capsule secretions. Surrounding the posterior wall of the brood pouch are a prominent albumen gland and a mucus (shell) gland. The single opening of the pallial oviduct is situated close to its anterior extremity. The condition found in *P. antipodarum* agrees well with that described for *P. jenkinsi* by Patil (1958), and Fretter & Graham.

(2) *Potamopyrgus estuarinus* and *P. pupoides* (Fig. 15e)

In these 2 species the form of the female system is identical and differs markedly from that of *Potamopyrgus antipodarum* in the structure and function of the lower section which is dominated by the strongly developed capsule gland. The ovary, oviduct, bursa copulatrix and receptaculum seminis are similar in size, shape and position to those of *P. antipodarum*, and in fertilized individuals the receptaculum seminis has a vivid, white appearance, given to it by masses of sperm packed inside. Both the diverticulae communicate with the spermathecal duct, a straight tube with a muscular wall, which opens to the anterior of the mantle cavity and is completely separate from the capsule gland above. This is unlike the condition found in *Hydrobia*, where the capsule gland forms the pallial oviduct, with the spermathecal duct running along its ventral surface only partially separated by longitudinal folds of tissue. Immediately in front of the bursa copulatrix is the albumen gland whose lumen is continuous with that of the capsule gland. Although the exact course of the eggs through the system has not been established it seems probable that the capsule

gland does not function as a pallial oviduct. Evidence from dissections and serial sections indicates that it has no anterior opening to the mantle cavity, nor any major connection with the spermathecal duct or oviduct (Fig. 15e) and developing eggs have never been found in its lumen. It is assumed, therefore, that eggs pass into the spermathecal duct which would act as the pallial oviduct as proposed by van der Schalie & Getz (1962) for *Pomatiopsis cincinnatiensis*.

The eggs of *Potamopyrgus estuarinus* and *P. pupoides* are spherical with a granular appearance, possess a thick (15 μ), striated shell, have no organs of attachment, and are laid singly. Eggs of *P. estuarinus* have a diameter of about 200 μ, whereas those of *P. pupoides* are larger, with a diameter of about 370 μ.

Gametogenesis has been observed in collections of *Potamopyrgus estuarinus* made in January, May, August, September and December and it seems probable therefore that it occurs throughout the year. Less is known regarding *P. pupoides* but females containing developing ova have been observed in spring and summer.

Chromosome numbers

Squashes of male and female gonads from the 3 species, including *Potamopyrgus antipodarum* from parthenogenetic and sexually reproducing populations, were examined to determine chromosome numbers. Interpretation of ovarian material was difficult but testis squashes included cells at various stages of spermatogenesis and could be readily interpreted. Chromosomes could be distinguished with some difficulty in early prophase and were most clearly counted in late prophase and metaphase. In all 3 species the diploid number 2n=24 was found and male gametes possessed the haploid complement n=12.

As a rule, chromosome numbers in the Prosobranchia tend to be conservative (Patterson, 1967), and this is clearly the case in *Potamopyrgus*.

Amino Acid Composition of Shell Periostracal Protein

The use of amino acids from molluscan shell protein for phylogenetic and taxonomic purposes is a very recent development, and preliminary studies have indicated that it could be a useful taxonomic technique (Degens, 1967; Ghiselin *et al.*, 1967). The molluscan shell is produced by secretion of precursors from the epithelial tissue in specialized areas of the mantle, and may consist of several layers. The outer layer or periostracum is not calcified and consists of over 95% protein (Degens, 1967). The inner layers of the shell are calcareous and include a proteinaceous matrix which represents less than 1% of the mineralized shell layers in the Gastropoda (Hare & Abelson, 1965).

As a species is defined, in part, by its distinct genetic composition differing from that of other species, and as proteins are genetically determined, genetic divergence between species will be displayed by differences in protein composition. In this investigation, amino acid analyses of periostracal protein have been made using ion exchange chromatography. Periostracum was chosen for two main reasons:

(*a*) It is easy to obtain relatively large quantities of material compared with minimal amounts of matrix protein.

(*b*) Shell ornamentation is periostracal, and comparisons of amino acid composition of smooth and spiny shells is of interest.

Snails from 2 populations of *Potamopyrgus estuarinus*, 1 of *P. pupoides* and 4 of *P. antipodarum* were examined (Table 6) and the results of analyses are presented in Table 7. Reproducibility of results was tested on 2 samples of *P. estuarinus*

TABLE 6. Material used for shell protein analysis.

Sample	Species	Locality	Shell form
1	*P. pupoides*	Wananaki B*	Smooth
2 a	*P. estuarinus*	Huia B	Smooth
2 b, c	*P. estuarinus*	Huia B	Smooth
3	*P. estuarinus*	Heathcote B	Smooth
4	*P. antipodarum*	Dannevirke	Smooth
5	*P. antipodarum*	Lake Pupuke	Spiny
6	*P. antipodarum*	Whangarei	Smooth & spiny
7	*P. antipodarum*	Lake Tutira	Smooth
8	*P. antipodarum*	Lake Tutira	Spiny

* B = brackish water.

from Huia (Table 7, 2a, 2b, 2c). When 2 identical runs were made on the sample (2b, 2c) the mean variation between amino acid values was 0·26% (range 0·01–0·63%). The mean variation between the same amino acids from 2 different samples from the same locality (2a, 2b) was 0·71% (range 0·11–2·8%). This variation incorporates differences between specimens, and errors introduced by decalcification, chromatography and data handling.

Marked differences in amino acid concentrations were found between Huia and Heathcote samples of *Potamopyrgus estuarinus*, glycine, proline, tyrosine and phenylalanine being greatly reduced in the latter, whereas most others showed corresponding increases in proportions. Values for *P. pupoides* corresponded closely to those of *P. estuarinus* from Huia, apart from a lower proportion of tyrosine. A wide range of variation was found in *P. antipodarum*, and no relationship between amino acid concentration and shell ornamentation was apparent. This is clearly demonstrated by comparing the extreme shell forms represented by Lake Pupuke and Dannevirke samples. In these, with the exception of tyrosine, relative proportions of amino acids are of a similar order. The presence of increased tyrosine in spiny shells is probably of no significance however, as high concentrations are also found in the smooth shells of *P. estuarinus*. Clearly, the New Zealand species cannot be distinguished by comparing the proportions of amino acids in shell periostracum as a high degree of intra-specific variation is found, paralleling the wide range of variation in macroscopic shell morphology.

The presence of considerable variation in the proportions of amino acids in the periostracum of *Potamopyrgus* species reinforces similar findings obtained in other studies. Hare (1963) found that periostracum showed more variation in amino acid composition than any other structural unit of the shell, and showed

TABLE 7. Ratios of periostracal amino acids in the 3 species of *Potamopyrgus*, expressed as percent total amino acids.

Amino acid	*P. pupoides*	*P. estuarinus*				*P. antipodarum*				
	1	2a	2b	2c	3	4	5	6	7	8
Aspartic acid	12·1	12·9	11·5	10·9	14·9	13·3	12·7	11·5	11·7	9·9
Threonine	4·4	3·5	3·2	3·2	4·5	4·6	4·4	3·2	4·8	5·5
Serine	5·3	4·4	4·1	4·0	5·3	4·7	4·4	3·5	5·1	6·7
Glutamic acid	7·0	6·8	6·1	6·4	8·6	7·4	7·6	5·2	7·4	8·5
Proline	4·8	4·7	5·4	5·8	2·2	2·4	2·3	3·6	4·5	5·4
Glycine	32·9	35·7	34·2	34·2	26·6	31·9	28·9	40·1	26·9	20·5
Alanine	7·0	5·7	5·4	5·2	7·7	4·4	7·1	4·1	8·7	11·0
1/2 Cystine	T*	T	T	T	T	T	T	T	T	T
Valine	4·5	4·1	4·4	4·0	6·0	5·6	5·0	3·4	4·4	6·2
Methionine	0·7	0·7	0·5	0·5	0·8	0·8	0·6	0·2	0·5	1·0
Isoleucine	2·5	2·3	2·1	2·1	2·8	2·7	2·8	1·8	3·0	3·7
Leucine	4·6	4·3	4·0	4·0	5·4	5·8	5·7	4·0	5·5	6·0
Tyrosine	2·4	6·2	6·9	7·1	3·7	4·1	6·4	4·8	3·2	3·2
Phenylalanine	5·5	4·5	4·1	4·7	4·3	5·4	5·1	6·4	5·5	4·6
Lysine	2·7	2·1	4·9	4·3	3·4	3·2	2·9	3·4	4·4	3·7
Histidine	0·4	0·2	0·3	0·2	0·1	0·6	0·2	1·1	0·7	0·3
Arginine	3·2	1·6	2·7	3·3	3·6	3·1	3·9	3·8	3·5	3·7

* T = trace.

that samples from the growing edge, around the periphery of a single specimen of *Mytilus californianus* may vary 10–15% in numbers of residues of many amino acids. Clearly defined differences in amino acid composition of periostracum between individuals of the brachiopod *Laqueus californianus* have also been demonstrated by Jope (1967).

An important source of amino acid variation may be protein heterogeneity, i.e., more than 1 protein may contribute to the periostracum as suggested by Hare (1963), Degens *et al.* (1967) and Jope (1967). Ghiselin *et al.* (1967) found that environmentally controlled variation in the amino acid composition of periostracum is sufficient to mask genetic differences in many cases. Recently, Hare & Meenakshi (1968) have reported that changes occurred in the proportions of periostracal amino acids of *Potamopyrgus jenkinsi* raised in the laboratory at different salinities. In particular they found an increase in the ratio of glycine to the acidic amino acids with decreasing salinity. However, no similar relationship was evident when the brackish water species *P. estuarinus* and *P. pupoides* were compared with *P. antipodarum* from fresh water.

Environmental Relationships

Distribution and general ecology

(1) *Potamopyrgus estuarinus.*

Potamopyrgus estuarinus has a clearly circumscribed habitat, and is confined to brackish water. Commonly it is found near the mouths of streams and rivers entering harbours, where the water is of fluctuating salinity. Frequently, the snails live a semi-terrestrial existence on mud flats or muddy banks adjacent to river

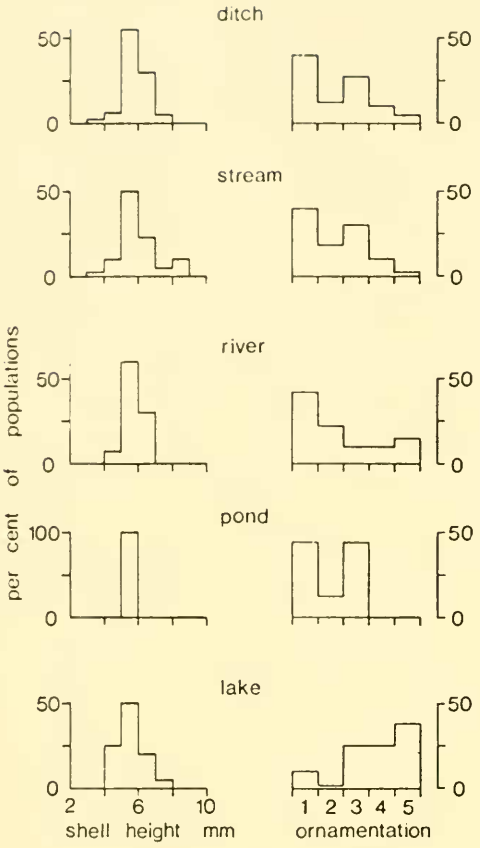

FIG. 16. Relationship between shell size, ornamentation and habitat in 97 populations of *Potamopyrgus antipodarum*. Key to shell ornamentation classes: 1—all snails smooth shelled; 2—most smooth; 3—half smooth, half spiny; 4—most spiny; 5—all spiny.

channels, or in harbour backwaters and salt swamps. In these situations they may lie exposed to the air for over half a tide cycle, and for the other half live in water of high salinity. The snails are inactive when exposed on mud flats, and may lie on the surface of the mud, be partially buried, or be grouped gregariously alongside or under stones, wood, etc. Snail densities of up to 884,000 per m^2 have been recorded in the Heathcote estuary.

Other snails remain immersed throughout the tide cycle, and may occupy various substrates including sand, mud, the upper and lower surfaces of stones, and clumps of weed. In river estuaries, snails are normally most abundant towards the seaward end, where salinities remain high.

Many past reports of the finding of *Potamopyrgus antipodarum* in brackish water undoubtedly refer to *P. estuarinus*.

(2) *Potamopyrgus pupoides*.

Potamopyrgus pupoides is confined to brackish water, and is frequently found in association with *P. estuarinus* in river estuaries, but is less frequently found on mud flats where it would be exposed to the air for regular periods of time. *P. pupoides* exhibits no marked substrate preferences and is found on stones, mud, and among living and decaying vegetation. Frequently, it is abundant in estuaries on a substrate of smooth, clean sand.

(3) *Potamopyrgus antipodarum*.

Potamopyrgus antipodarum occurs throughout New Zealand in a wide variety of habitats, including lowland rivers, stony streams, creeks, ditches, estuaries, ponds, lakes, springs, wells and permanent seepage. One of the few freshwater habitats it seems unable to colonize is the temporary pond as the snails apparently lack resistant stages capable of carrying them over long dry seasons.

Within the *Potamopyrgus antipodarum* complex a number of relationships between particular shell forms and geographical or ecological distribution are evident, but none of these relationships appears to be so well circumscribed, or clearly defined, as to warrant taxonomic recognition of the populations concerned. The main trends found are:

(*a*) Many snails at high altitudes, and/or in relatively oligotrophic waters, have a much smaller adult size than most low-

TABLE 8. Salinity ranges at which the 3 species of *Potamopyrgus* have been found living.

Species	Salinity o/oo		Maximum Diurnal Range
	Maximum	Minimum	
P. antipodarum	26·4	0	17·7
P. pupoides	32·3	2·7	,,
P. estuarinus	34·8	2·7	,,

land populations. These snails are predominantly smooth shelled.

(*b*) Snails in many, but not all, populations north of Auckland attain a very large size, their shells sometimes exceeding 10 mm in height. This size increase is produced by an increase in the number of whorls, rather than by an increase in size of the whorls.

(*c*) There is a tendency for the shells of spiny shelled snails in many lakes and rivers to be more slender and strongly shouldered in the South Island than in the North.

Although laboratory rearing work has indicated that shell form is not a simple phenotypic response to environment, in some instances small size may be the result of reduced growth at low temperatures, or under poor food conditions. Conversely, higher temperatures may permit an increase in the rate and amount of growth, resulting in the attainment of large size.

No clear relationship between shell height or ornamentation, and different habitat types was found (Fig. 16), although many lake populations tend to consist predominantly of spiny snails, whereas smooth shelled snails are more abundant in running water.

Salinity relations

All 3 species of *Potamopyrgus* are found over a wide range of salinities, but only *P. antipodarum* is found in fresh water (Table 8).

In order to determine the range of salinities tolerated by each species, the responses of snails kept in water at 11 different salinities ranging from 0–33‰ salinity, were examined in the laboratory.

After 24 hours in the experimental situation all individuals of *Potamopyrgus estuarinus* and *P. pupoides* exhibited normal acitivity at all experimental salinities, 0–33‰ salinity, and *P. antipodarum* from fresh and brackish waters was active at up to 17·5‰ salinity. Some reduced movement of *P. antipodarum* was found at 21‰ salinity but in more saline water all snails withdrew completely into their shells, their opercula acting as physical barriers to exclude the water. After a further 24 hours in water of 3·5‰ salinity, all previously inactivated snails resumed normal activity.

In the field, the highest salinity at which *Potamopyrgus antipodarum* has been found living is 26·4‰, slightly higher than the greatest salinity at which activity occurred under experimental conditions. It is possible that some intraspecific variation is found in *P. antipodarum* with respect to salinity tolerance as was found in *P. jenkinsi* by Duncan & Klekowski (1967). Although *P. estuarinus* and *P. pupoides* have not been found in fresh water in the field, they were able to exist

in it for several months in the laboratory. Perhaps they are unable to reproduce or develop in freshwater.

The ability to tolerate a wide range of salinities is clearly advantageous to all 3 species, as rapid changes in salinity are regularly encountered in the estuarine reaches of rivers frequently inhabited by them.

Amphibious behaviour

Apart from inhabiting waters of different salinities, *Potamopyrgus antipodarum* and *P. estuarinus* are frequently found in contrasting physical environments. *P. estuarinus* is often abundant on high-tidal mud flats bordering streams where snails may be exposed to the air for an appreciable period of each tide cycle, whereas *P. antipodarum* always remains in the water. Laboratory experiments were carried out to compare the behaviour of the 2 species when a choice of 3 substrata, submerged mud, exposed water saturated mud, and slightly damp mud, was offered to them.

Results of experiments are shown in Fig. 17. In Experiment 1 snails were distributed evenly throughout the box at the start of the experimental period and a single examination of their subsequent distribution was made after 17 hours. In Experiment 2 all snails were placed in the submerged section of the box on commencing the experiment, and their distribution was examined after 1, 2, 24 and 72 hours. Similar results were obtained in both studies. A clear behavioural difference between the 2 species was apparent, the majority of *Potamopyrgus estuarinus* finally selecting the driest substrate, whereas almost all *P. antipodarum* remained in the water, or were buried in the water-saturated mud of the middle zone. Movement of *P. estuarinus* from the water to the dry upper zone is clearly shown in Experiment 2 (Fig. 17).

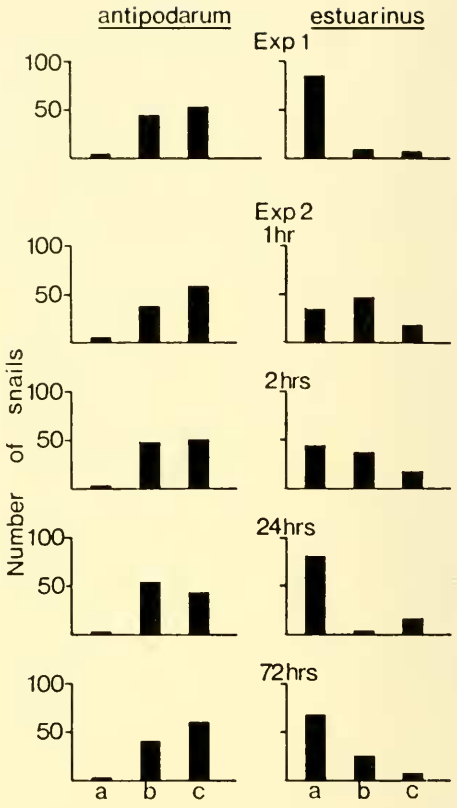

FIG. 17. Selection of submerged and exposed substrata by *Potamopyrgus estuarinus* and *P. antipodarum* in laboratory experiments. Expt. 1, snails initially distributed throughout box; examined after 17 hours; Expt. 2, all snails initially submerged. Substrata: a = damp, exposed mud; b = saturated mud; c = submerged mud.

The relatively large numbers of *Potamopyrgus antipodarum* occupying the middle zone of water-saturated mud, is probably explained by the presence of favourable respiratory conditions at the air-water interface in this zone. A similar situation is regularly found in still water laboratory cultures lacking vegetation, in which the majority of snails move up the sides of the containers and settle immediately beneath the surface film.

Although in the experimental situation most *Potamopyrgus estuarinus* remained

TABLE 9. Time survived by snails in a still, dry atmosphere, and on a dry substratum.

Species	All alive (hours)	First death occurs (hours)	All dead (hours)
P. antipodarum	0–6	6–12	30
P. estuarinus	0–6	6–12	42
P. pupoides	0–6	6–12	24

permanently in the dry zone and exhibited no active movement back to the water, in their natural habitat they do not normally remain exposed to the air for more than a few hours at a time, as tidal movements ensure they will be covered at regular intervals. It is essential that the habitat should be submerged regularly as snails cannot move about and feed when the substrate is dry. One consequence of this positive movement out of water could be to prevent colonization of permanent river channels, and so effectively isolate populations of *P. estuarinus* and *P. antipodarum* in many areas where their ranges overlap.

Effect of desiccation and starvation

Associated with the colonization of a non-aquatic habitat is the problem of preventing desiccation. This is likely to be of considerable importance to a primarily aquatic species such as *Potamopyrgus estuarinus* which is periodically exposed to the air. *P. antipodarum* although strictly aquatic, sometimes inhabits bodies of fresh water with fluctuating water levels, or which can be drained by natural or artificial means. In such situations, if the snails are unable to withstand exposure to air, whole populations may be quickly destroyed.

Laboratory experiments were designed to examine the effect of desiccation and starvation on the 3 species, (*a*) in dry air and on a dry substratum, and (*b*) on a damp substratum in moisture saturated air.

The time survived by the 3 species in a still, dry atmosphere is shown in Table 9. Similar responses were obtained from all species.

Survival times of snails in a moisture-saturated atmosphere, and on a damp substrate is shown in Fig. 18.

Direct observations indicated that snail tissues did not become rapidly desiccated under these conditions, and that at all times some moisture was maintained within the shells of the snails. On a damp, but non-submerged substrate, however, movement, and consequently feeding, cannot occur and therefore death probably results from starvation combined with desiccation. Deaths of *Potamopyrgus antipodarum* and *P. pupoides* are therefore attributed to the combined effects of desiccation and starvation. However, the situation was very different for *P. estuarinus* which apparently entered a state of dormancy or aestivation, and had a high survival rate over a long period. Individuals which remained dormant up to 50 days resumed activity when transferred to a vessel of water.

Little is known about aestivation in the Prosobranchia although short term aestivation does occur in some Pomatiasidae

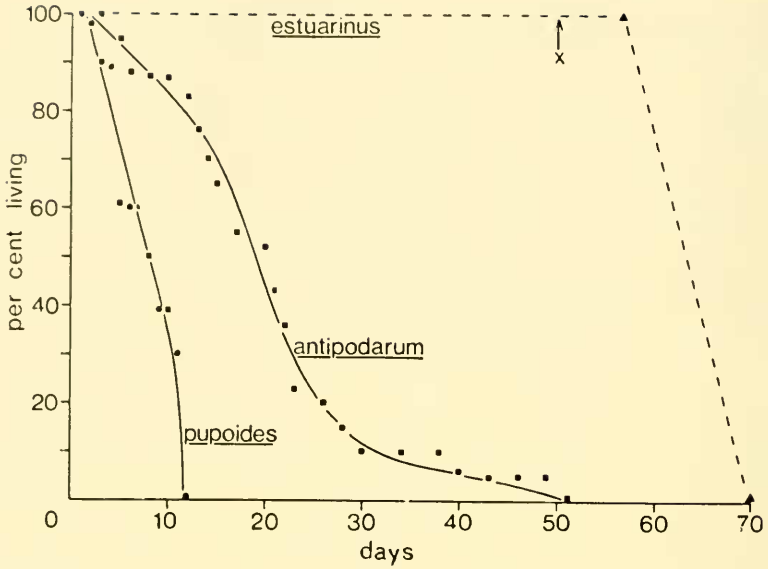

FIG. 18. Survival time of snails on a damp substratum at 20–25° C. Circles = *Potamopyrgus pupoides*; squares = *P. antipodarum*; triangles and broken line = *P. estuarinus*. X–10 snails placed in water (all resumed activity).

(Hunter, 1964) and Hydrobiidae (Dundee, 1957). Quick (1920) found that *Hydrobia* spp. could withstand long periods of exposure and survive in an apparently desiccated state, and Dundee (1957) has noted that dormancy occurs in the amphibious *Pomatiopsis lapidaria* in very cold or hot and dry weather. This evidently ensues when there is a lack of sufficient available moisture, the snails lying with their opercula inserted well into the shell apertures during the inactive period, and becoming reactivated with the onset of rain. Clearly the ability to withstand long periods of exposure out of water is advantageous to snails such as *P. lapidaria* and *P. estuarinus* which possess an amphibious way of life, and may suffer prolonged periods of exposure.

DISCUSSION

The species problem

As a result of this study, 3 species of *Potamopyrgus* are now recognized in New Zealand. Two of these, *P. pupoides* and *P. estuarinus*, are clearly distinguished using morphological, reproductive, and ecological evidence, but *P. antipodarum* contains a heterogeneous assemblage of forms embracing all the purely freshwater populations. It includes a wide range of morphological variants, as well as differing reproductive forms, and is found under diverse environmental conditions. In the past, many of the forms included in this species have been considered morphologically distinct enough to be recognized as separate species, or to have had restricted geographical distributions allowing them subspecific recognition. This study has shown that continuous morphological variation exists within the complex, and that discrete geographical distributions of taxonomic subgroups, consistent with the definition of the subspecies (Mayr, *et al.*, 1953) are difficult to find. A gradation in reproductive forms, through populations with few males, to total parthenogenesis is also

found, and the possession of these different states, apparently unassociated with particular morphological forms, or the occupation of particular habitats adds further to the difficulty of discriminating distinct taxonomic units within the complex.

The possession of a parthenogenetic mode of reproduction by a large proportion of the populations of *Potamopyrgus antipodarum* is perhaps the major factor responsible for so much of the taxonomic uncertainty that has occurred in the past, and it has permitted the formation of many reproductively isolated clones in which divergent evolution has been able to occur. Furthermore, Struhsaker (1968) in a discussion of shell variation in *Littorina* spp. suggested that species which are viviparous could be expected to have more intra-specific variation because of decreased distribution (dispersal) and restricted mating. This would result in isolated populations, whereas strictly oviparous populations with widespread larvae should be least variable. This contention is supported by the findings in the present study, the 2 oviparous species, *P. estuarinus* and *P. pupoides* possessing limited morphological variability compared with the extreme plasticity of the ovoviviparous *P. antipodarum*.

Reproduction by parthenogenesis also poses nomenclatural problems. The biological species definition (e.g. Mayr, 1963, " Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups "), applies only to sexually reproducing organisms, and it is generally accepted that the taxonomy of obligatory parthenogens therefore must be arbitrary. In the past it has been based primarily on morphological, ecological and biogeographic evidence. The occurrence of sexual reproduction and parthenogenesis in the *Potamopyrgus antipodarum* complex poses further problems. White (1954) and Mayr (1963) have pointed out that it is illogical to recognize parthenogenetic and bisexual " races " of the same species, irrespective of the morphological resemblances between the genotypes, and they considered that such forms were better recognized as sibling species, if they were indistinguishable by ordinary taxonomic criteria. On the other hand, Mayr *et al.*, (1953) have agreed that it is unjustifiable to give nomenclatural recognition to forms with temporary or facultative parthenogenesis. In *P. antipodarum*, sexually reproducing and parthenogenetic forms are connected by intermediates possessing limited numbers of males, and it seems likely that in such populations both parthenogenesis and sexual reproduction may occur.

In view of this lack of a sharp division between reproductive types, and the presence of continuous morphological variation within the complex, it seems most sensible to consider the whole range of intergrading populations as a single species.

The suitability of an evolutionary species concept such as that of Simpson (1961); " An evolutionary species is a lineage evolving separately from others and with its own unitary evolutionary role and tendencies ", which is not hampered by the static restrictions of genetical (biological) definitions, is evident in a situation of this kind.

Parthenogenesis and evolution in *Potamopyrgus*

Parthenogenesis was first discovered in molluscs by Boycott (1919), in *Potamopyrgus jenkinsi*, and later in the American viviparids *Campeloma rufum* and *C. decisum* by van Cleave & Altringer (1937) and Medcof (1940), and in 4 species of Melaniidae by Jacob (1957). Parthenogenesis in all these species is thelytokous (female diploid parthenogenesis) and of the apomictic type, (i.e., it is ameiotic and

neither chromosome reduction nor fusion of nuclei takes place in the egg). In many animals, parthenogenesis is frequently accompanied by polyploidy (Suomalainen, 1950), and of the molluscs examined, 3 species of *Melanoides* are polyploid and 1 species is diploid (Jacob, 1957). It has been stated that *P. jenkinsi* exists as 2 distinct genotypes, a diploid race in Europe (2n=20–22) and a tetraploid race in Great Britain (2n=36–44) (Sanderson, 1940), but Suomalainen (1950) and Patterson (1967) consider that this needs reinvestigation.

In the *Melanoides* species, parthenogenesis is obligatory, although small numbers of sexually non-functional males are found in 2 species (0·01–3·0% of populations). Obligatory parthenogenesis has been considered the rule in *P. jenkinsi* also, although a single male has been found by Patil (1958). Males occur sporadically in populations of *C. rufum* (about 1%) and are scarce or rare in 3 other species of *Campeloma* about whose reproduction little is known (Mattox, 1938; van der Schalie, 1965).

In *Potamopyrgus antipodarum* parthenogenesis is apomictic (2n=24) and polyploidy has not been observed in any snails examined. In populations where males are present, they are always sexually functional and male gametes possess the haploid chromosome number (n=12). Circumstantial evidence therefore suggests that parthenogenesis is not necessarily obligatory in all populations of *P. antipodarum*, and that where it is not, and fertilization occurs, a reduction in the chromosome number of ova must occur, so as to maintain the diploid number and not produce a triploid form. Perhaps the stimulus bringing about meiosis in the developing egg is the occurrence of copulation, or the presence of the sperm in the female system. A situation closely paralleling that found in *P. antipodarum* has been described by Robertson (1966) in chrysomelid beetles of the genus *Calligrapha*. These possess extremely variable sex ratios, ranging from 1:1, to all female populations, and parthenogenesis in at least one species, *C. scalaris*, is facultative.

The origin of parthenogenesis in all cases examined is considered to be from sexually reproducing forms, i.e. it is a secondarily derived condition (Mayr, 1963; Suomalainen, 1961), and Mayr has stated, that with the apparent exception of the bdelloid Rotifera, virtually every case of parthenogenesis in the animal kingdom is probably of very recent origin. A recent origin for parthenogenesis in *Potamopyrgus antipodarum* is indicated by the continued presence today of bisexual as well as parthenogenetic populations, and by the retention of the sperm channel, bursa copulatrix and receptaculum seminis in the reproductive system of parthenogenetic females. A parallel situation is found in parthenogenetic species of *Calligrapha* which retain a non-functioning spermatheca (Robertson, 1966).

The advantages parthenogenesis gives to a species have been discussed by several workers (White, 1954; Mayr, 1963; Tomlinson, 1966), who have concluded that it is particularly advantageous to animals inhabiting temporary or marginally suitable habitats where population densities are often low. In these situations it permits a single individual to commence breeding without requiring a mate and the reproductive capacity of the clone will be doubled as all individuals will be egg producing females. Thus, parthenogenesis increases productivity by allowing rapid build up of populations, and therefore it can be of definite, short term advantage to forms possessing it. Because no exchange of genes is possible, a parthenogenetic species frequently will continue to diverge as different mutations establish in different lines of descent. Thus, a high degree of variability will

ultimately result within many parthenogenetic species, variability which will not necessarily be correlated with geographic distribution in the same way as in a sexually reproducing form. This is what is found in *Potamopyrgus antipodarum*. Suomalainen (1961, 1962) has speculated on the ways in which mutations may be expressed in apomictic parthenogenetic animals, and his theoretical mechanism could possibly apply in the present situation. He argues that increasing heterozygosity will occur between more and more gene pairs (because elimination of recessive mutations by natural selection is impossible) until the 2 chromosome sets can no longer be considered diploid or polyploid in a genetic sense. This will reduce obstacles to the expression of the mutations present in them, and may thus, in part, even allow the formation of morphologically divergent biotypes. Further, with a continuous increase in the degree of heterozygosity, an apomictically parthenogenetic form gets an ever increasing chance to benefit from heterosis (hybrid vigour). This may therefore provide the basis for the apparently great adaptiveness and dispersive ability of many parthenogenetic forms (e.g., *P. antipodarum*), although it is in direct contrast with the widely held view that parthenogenesis leads to a lack of adaptability, and long term disadvantage (White, 1954).

Probable steps in the evolution of *Potamopyrgus* are shown in Fig. 19. *P. estuarinus* and *P. pupoides* possess the primitive features, smooth shell, sexual reproduction and oviparity, and are confined to brackish water, whereas in *P. antipodarum* shell ornamentation, parthenogenesis and ovoviviparity have developed, probably concurrently with the invasion of fresh water. Further divergent evolution has occurred and is occurring within isolated parthenogenetic populations of *P. antipodarum*, resulting in a high degree of genetic and phenotypic variability.

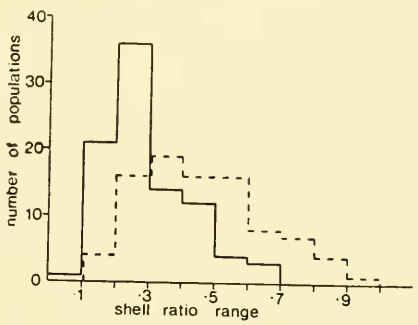

FIG. 19. Postulated steps in the evolution of the New Zealand species of *Potamopyrgus*.

The relationship of *Potamopyrgus antipodarum* to the European species *P. jenkinsi*

Potamopyrgus jenkinsi made a sudden appearance in Europe, first being described by E. A. Smith in 1889, although it may have been present as early as 1859. Its origin is uncertain and has been the subject of considerable speculation which has been reviewed by Adam (1942), Bondeson & Kaiser (1949) and Fretter & Graham (1962). The subsequent distribution of *P. jenkinsi* through Europe has also been discussed by these authors and others, e.g., Hubendick (1950).

Attempts to explain the sudden appearance of *Potamopyrgus jenkinsi* in Europe have been made by various authors, and 2 possible explanations have been suggested; (*a*) that it arose by mutation (Steusloff, 1927; Boettger, 1949), and (*b*) that it had been introduced from elsewhere. Bondeson & Kaiser (1949) have hypothesized a possible Australian origin on account of the close resemblance to the Australian species (?) *P. pattisoni*, and Boettger (1951) has suggested a New Zealand origin for *P. jenkinsi* as he considered its shell characters identical with those of *P. badia* (=*P. antipodarum*) from the South Island of New Zealand.

As a result of the present study on the New Zealand species of *Potamopyrgus*, it is possible to make a more critical comparison with *P. jenkinsi* than has been possible in the past. In doing this, information contained in the literature has been evaluated, and in addition, living and preserved material of *P. jenkinsi* from Scotland has been examined.

The shells of *Potamopyrgus jenkinsi* are variable in shape, size and ornamentation, although not as variable as those of *P. antipodarum* (T. Warwick, pers comm.), and cannot be differentiated from those of some *P. antipodarum*. Ornamentation is purely periostracal, and exists in many degrees of strength, from a faint line to a well marked spinous keel (Warwick, 1944; Fretter & Graham, 1962). Rearing experiments (Boycott, 1929; Robson, 1926; Warwick, 1944), have shown that as in *P. antipodarum* shell ornamentation of progeny does not necessarily follow that of the parent, but despite considerable speculation the mechanism controlling shell ornamentation remains unknown (Warwick, 1944; 1952; Bondeson & Kaiser, 1949).

The radula of *Potamopyrgus jenkinsi* has been described by Woodward (1892) and Krull (1935), and new material has been examined in this study. The shape of the teeth, cusp formulae, radular length, and number of rows of teeth lie within the ranges found in *P. antipodarum*.

Potamopyrgus jenkinsi exhibits considerable variability in colour and pigmentation of the head and mantle (Robson, 1920), and it cannot be separated from *P. antipodarum* on this basis, or on the structure of the operculum, or the form of the female reproductive system. Both species are ovoviviparous, and *P. jenkinsi* is considered to be parthenogenetic like many populations of *P. antipodarum*. A single male of *P. jenkinsi* has been described by Patil (1958), and it is possible that a situation similar to that found in *P. antipodarum* in which variable numbers of males occur in some populations, also exists in *P. jenkinsi*. The anatomy of the male reproductive system in the solitary male *P. jenkinsi* was identical to that of *P. antipodarum*, apart from one minor difference, the presence of a small swelling in the upper vas deferens, described as the seminal vesicle by Patil. No such swelling has been found in *P. antipodarum*. Both species reproduce throughout the year, an unusual condition in freshwater Mollusca (Fretter & Graham, 1962), and although a maximum of only 35–40 embryos has been recorded in the brood pouch of *P. jenkinsi*, compared with over 100 in some individuals of *P. antipodarum*, this is unlikely to be of systematic significance. Rather, it is probably a function of the size of the snail (and therefore the brood pouch) as *P. jenkinsi* rarely exceeds about 5 mm in shell height, whereas *P. antipodarum* may attain a height greater than 10 mm.

Considerable variation in ecology is also found in the 2 species. *Potamopyrgus jenkinsi* was initially found in brackish water (1889) and has since colonized inland waters throughout Europe and the British Isles, first having been recorded in fresh water in England in 1893 (Hunter & Warwick, 1957). *P. antipodarum*, similarly, is found in fresh and brackish water, although it is primarily a freshwater species and has certainly been established in that environment for a much longer period than has *P. jenkinsi*. Salinity records and experimental work have shown that both species possess a high degree of euryhalinity and can tolerate considerable and rapid changes in salinity. Maximum salinities at which *P. jenkinsi* can reproduce, 12–18‰, (Duncan & Klekowski, 1967) correspond closely to the value of 17·5‰, obtained in this study at which normal activity of *P. antipodarum* ceases and the snails withdraw into their shells. Both species tolerate waters with

high and low calcium content, and live in a variety of still, and running water habitats, on hard and soft substrates, and amongst vegetation.

To conclude, no significant morphological or biological differences between the 2 nominal species have been found to date, and the evidence available therefore suggests that they are the same. However, the systematics of the Australian hydrobiids, some of which are or have been placed in *Potamopyrgus* and related genera, are not clear at present and their relationship to the New Zealand species and to *P. jenkinsi* cannot be clarified until after comprehensive morphological and biological studies have been carried out on them. The presence of related genera and species in Australia (Williams, 1968) and in the South Pacific (Hubendick, 1952), indicates that New Zealand is near the centre of *Potamopyrgus* evolution, however, and it seems most likely that the European snails have been introduced from the Australasian region.

ACKNOWLEDGEMENTS

I wish to thank Dr. Tim Brown, Dr. W. C. Clark and Mr. L. Gurr of Massey University, and Drs. R. K. Dell and W. F. Ponder of the Dominion Museum, Wellington for their assistance and interest during the course of this work.

The help of Dr. G. G. Midwinter with the biochemical analyses, Miss Pauline Campbell who did much of the sectioning of snails, and Mr. Tom Warwick who sent me living specimens of *P. jenkinsi* from Scotland has been greatly appreciated.

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RÉSUMÉ

LES ESPÈCES DE *POTAMOPYRGUS* DE NOUVELLE-ZÉLANDE

(Gastropoda: Hydrobiidae)

M. Winterbourn

Dans sa revision du genre, Suter (1905) reconnaît 6 espèces et 3 sousespèces de *Potamopyrgus* dans les deux principales îles de Nouvelle-Zélande, mais l'étude présente a mis en évidence qu'il n'y a seulement que 3 espèces. Ce sont: *P. antipodarum* (Gray 1843), *P. pupoides* Hutton 1882 et une espèce précédemment non reconnue **P. estuarinus** n. sp.

Potamopyrgus estuarinus et *P. pupoides* sont ovipares, possédant des coquilles lisses non ornementées et se confinent aux eaux saumâtres, tandis que *P. antipodarum* est ovovivipare, a une coquille extrêmement variable par sa taille, sa forme et son ornementation et habite aussi bien les eaux douces que saumâtres. Les populations de *P. antipodarum* peuvent comprendre uniquement des femelles parthénogénétiques ou contenir un pourcentage variable de mâles sexuellement fonctionnels. L'élevage de *P. antipodarum* au laboratoire a montré que les individus ne conservent pas forcément d'une génération à l'autre les caractères ornementaux de la coquille et que la forme et l'ornementation de la coquille ne dépendent pas à l'origine des facteurs du milieu. La coquille de *P. estuarinus* est indistingable de certaines coquilles de *P. antipodarum*, mais *P. pupoides* est facilement reconnaissable par sa petite coquille pupiforme.